Université de Montréal

Révision taxonomique de la famille des Harrimaniidae (Hemichordata: Enteropneusta) incluant les descriptions de sept espèces de la côte Est du Pacifique

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Ce mémoire intitulé :

Révision taxonomique de la famille des Harrimaniidae (Hemichordata: Enteropneusta) incluant les descriptions de sept espèces de la côte Est du Pacifique

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Résumé

Cette étude comparative est une révision de la famille des Harrimaniidae basée sur les caractères morphologiques d'espèces connues et nouvelles provenant des collections de William E. Ritter, Theodore H. Bullock et Kandula P. Rao rassemblées au cours du 20^{e} siècle. Les descriptions présentées ici portent le total des genres de cinq à neuf par l'ajout de *Horstia* n. gen., *Mesoglossus* n. gen., *Ritteria* n. gen et *Saxipendium,* un genre auparavant attribué à la famille monospécifique des Saxipendidae. Le nombre d'espèces est porté à 34 par la description de cinq nouvelles espèces du Pacifique oriental: *Horstia kincaidi, Mesoglossus intermedius*, *Mesoglossus macginitiei*, *Protoglossus mackiei* et *Ritteria ambigua*. La description d'une sixième espèce, *Stereobalanus willeyi* Ritter et Davis, 1904 (*nomen nudum*) est présentée ici pour la première fois, ainsi qu'une description abrégée de *Saxipendium coronatum*. Quatre espèces précédemment attribuées au genre *Saccoglossus* sont transférées au genre *Mesoglossus*: *M. bournei*, *M. caraibicus*, *M. gurneyi,* et *M. pygmaeus* et *Saccoglossus borealis* est transféré au genre *Harrimania.* Une hypothèse phylogénétique sur la famille des Harrimaniidae est émise, présentant l'évolution possible des caractères morphologiques au sein du groupe. Finalement, des notes sur la distribution géographique étendue mais discontinue de plusieurs espèces suggère que les entéropneustes auraient pu avoir une distribution ancienne continue et plus grande qui aurait été fragmentée par la suite.

Mots-clés: Taxonomie, révision systématique, morphologie, Enteropneusta, Hemichordata, Harrimaniidae, biogéographie

Summary

This comparative study is a revision of the family Harrimaniidae based on morphological characters of described and undescribed species from the collections of William E. Ritter, Theodore H. Bullock and Kandula P. Rao, gathered in the 20th century. The new descriptions bring the total number of genera to nine by the addition of *Horstia* n. gen., *Mesoglossus* n. gen., *Ritteria* n. gen and *Saxipendium,* a genus previously assigned to the monospecific family Saxipendidae The number of species is increased to 34, resulting from the description of five new species from the eastern Pacific: *Horstia kincaidi, Mesoglossus intermedius*, *Mesoglossus macginitiei*, *Protoglossus mackiei* and *Ritteria ambigua*. The description of a sixth species, *Stereobalanus willeyi* Ritter et Davis, 1904 (*nomen nudum*) is presented here for the first time and a brief description of *Saxipendium coronatum* is also presented. Four species previously assigned to the genus *Saccoglossus* are transfered to the genus *Mesoglossus*: *M. bournei*, *M. caraibicus*, *M. gurneyi,* and *M. pygmaeus*, while *Saccoglossus borealis* is transfered to the genus *Harrimania*. A phylogenetic hypothesis on the Harrimaniidae is postulated presenting the possible evolution of morphological characters within the group. Finally, notes on the wide but spotty distribution of several species suggest that the Enteropneusta may have once had a wider distribution that has since become fragmented.

Key words: Taxonomy, systematic revision, morphology, Enteropneusta, Hemichordata, Harrimaniidae, zoogeography

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Liste des sigles et des abréviations

a	anus
ac	amoeboid-like cells
ADNr	Acide désoxyribonucléique ribosomal
b	bouche
bp	branchial pore
bs	branchial sac
bv	blood vessel
c	collar
cc	collar canal
ch	caecum hépatique
cl	collar lumen
clm	collar longitudinal muscles
cm	circular muscle layer
cms	canal du mésocoele
cnd	corde nerveuse dorsale
co	coeur
cp	coelome périhémal
cpb	cavité péri-buccale
cv	cardiac vesicle
dm	dorsal mesentery
e	epithelia
fb	fente branchiale
g	glomérule / glomerulus
gb	gill bar
go	gonade / gonad
gr	genital ridge
m	mouth
md	mésentère dorsal
ms	mésocoele
mt	métacoele
nc	nerve cord
ncc	nerve cord crest
ncl	nerve cord lacunae
nf	nerve fiber layer
np	neuropore
nr	nerve root
opc	organe pré-oral cilié
p	proboscis
pb	pore branchial
pbd	peribuccal diverticula
pbr	parabuccal ridge
pc	proboscis coelom
pl	pharynx lumen
plm	proboscis longitudinal muscles
phd	periheamal diverticuluum
pp	pore du proboscis / proboscis pore
ps	péritoine viscéral
pt	protocoele
pv	proboscis vesicle
qp	queue post-anale
s	stomocorde / stomochord
sb	skeletal body

sbr	sac branchial
sc	skeletal cornua
sca	sinus cardiaque
se	septum
sk	skeletal keel
sl	stomochord lumen
sp	skeletal plate
sqp	squelette du proboscis
t	trunk
tlm	trunk longitudinal muscles
vc	ventral caecum
vm	ventral mesentery
vsd	vaisseau sanguin dorsal
vsv	vaisseau sanguin ventral

1. Introduction

1.1 BIOLOGIE

Les entéropneustes sont des vers benthiques exclusivement marins qui vivent, pour la plupart, dans les sédiments en zone peu profonde ou associés aux roches et aux crampons des algues laminaires. Certaines espèces ont également été trouvées en mer profonde sur les plaines abyssales (Holland, 2005, 2009) et près des sources hydrothermales (Woodwick et Sensenbaugh 1985). Ils sont présents partout sur le globe, mais la plupart des espèces ont été trouvées dans les eaux tropicales et sub-tropicales (Hyman, 1959). On sait très peu de choses en ce qui a trait à leur écologie et leur biologie, la plupart des espèces étant rares et peu étudiées.

Certaines espèces sont tubicoles et construisent des terriers en forme de "U" qui peuvent être repérés en zone intertidale par des tas d'excréments spiralés laissés à l'une des deux extrémités du terrier. Ces espèces présentent deux types de mode d'alimentation. Les espèces du genre *Saccoglossus* balaient la surface des sédiments à l'extérieur d'une des embouchures du terrier à l'aide de leur long proboscis, tandis que les espèces du genre *Balanoglossus* construisent plutôt une embouchure en forme d'entonnoir dans laquelle ils font tomber les sédiments, leur permettant ainsi de garder leur proboscis à l'intérieur du terrier (Hyman, 1959).

Certaines espèces ne construisent pas de terrier permanent et vivent simplement enfouies dans les sédiments, sous les roches ou parmi les racines des plantes, mais on ne sait que très peu de choses sur les espèces ayant ce mode de vie. Les entéropneustes s'alimentent de matière organique contenue dans les sédiments en transportant les particules de nourriture vers la bouche le long du proboscis à l'aide de cils et de mucus (Barrington 1940, Knight-Jones 1953, Thomas 1972). Quelques espèces, comme *Harrimania planktophilus,* s'alimentent aussi par filtration à travers les fentes pharyngiennes, à la manière des céphalocordés (Cameron, 2002).

Leur reproduction est de type sexué, mais certaines espèces comme *Glossobalanus crozieri* semblent se reproduire aussi par clonage en détachant leur

extrémité postérieure qui se regénère par la suite pour donner deux individus complets (Petersen & Ditadi, 1971). Les espèces de la famille des Harrimaniidae ont un développement de type direct, tandis que les espèces des autres familles produisent une larve tornaria planctonique semblable à la larve de certains échinodermes.

Les entéropneustes sécrètent plusieurs types de composés halogénés tels que les bromophénols et bromoindoles qui leur confèrent une odeur médicinale distinctive et qui ont, entre autres, pour fonction de repousser certains prédateurs et parasites (Higa *et al.* 1980).

1.2 ANATOMIE

La taille des entéropneustes varie de quelques dizaines de millimètres pour la plupart, à plus de 1,50 m pour *Balanoglossus gigas* (Spengel, 1893). Ils ont une symétrie bilatérale simple et un corps trimérique (voir figure 1 pour le schéma d'un entéropneuste). Chacune des trois régions corporelles contient une cavité coelomique séparée des autres par des septa; le protocoele au niveau du proboscis, le mésocoele au niveau du collet et le métacoele au niveau du tronc. Ces cavités coelomiques présentent des diverticules et des pores communiquant avec l'extérieur du corps. Le ou les pore(s) du protocoele se situe(nt) au niveau du pédoncule du proboscis, ceux du mésocoele sont sous forme de canaux qui s'ouvrent au niveau de la première paire de branchies et le métacoele est percé de pores oesophagiens. Une caractéristique distinctive des entéropneustes est le diverticule de la cavité buccale qui se prolonge antérieurement à l'intérieur du proboscis. Cette structure se nomme la stomocorde et a souvent été comparée à la notocorde des céphalocordés de par sa structure similaire. La bouche est ventrale, à la jonction du proboscis et du collet. L'anus est terminal.

Les entéropneustes possèdent des branchies et des fentes pharyngiennes dorso-latérales supportées par un squelette de collagène. Une autre pièce squelettique aussi faite de collagène sert de support au proboscis. Les gonades sont situées en deux ou

quatre rangées dorso-latérales qui peuvent être proéminentes ou non, selon les espèces.

Le système circulatoire est composé des vaisseaux sanguins principaux, l'un ventral, l'autre dorsal, ainsi que d'un organe unique, le coeur-rein. Cet organe est composé d'un péricarde, d'un vaisseau sanguin et de glomérules. Les pulsations du coeur sont produites par des fibres musculaires insérées sur la stomocorde, qui sert de support à ce complexe.

Le système nerveux est diffus. On dénote toutefois un renflement de fibres nerveuses le long de la ligne médiane dorsale, qui peut parfois prendre l'aspect d'un tube plus ou moins complet, semblable à celui des céphalocordés. Les entéropneustes possèdent une musculature très fine, les muscles les plus distinctifs se trouvant dans le proboscis.

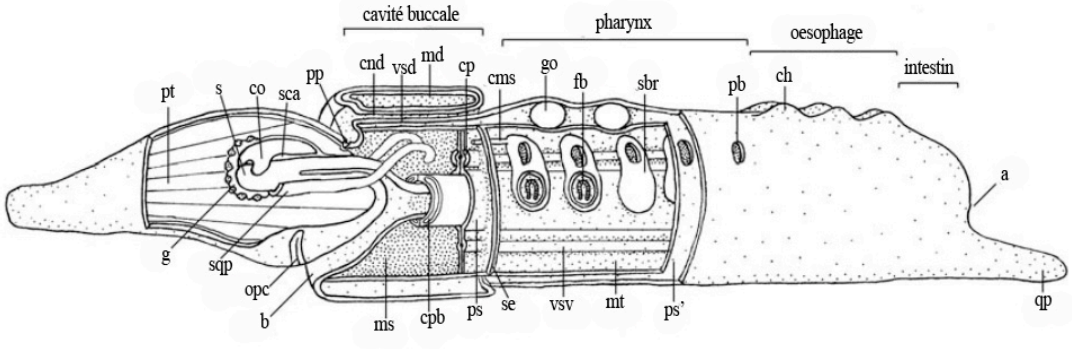

Figure1. Schéma d'un entéropneuste généralisé, modifié de Cameron, 2005. a, anus; b, bouche; ch, caecum hépatique; cms, canal du mésocoele; cnd, corde nerveuse dorsale; co, coeur; cp, coelome périhémal; cpb, cavité péri-buccale; fb, fente branchiale; g, glomérule; go, gonade; md, mésentère dorsal; ms, mésocoele; mt, métacoele; opc, organe pré-oral cilié; pb, pore branchial; pp, pore du proboscis; ps, péritoine viscéral; pt, protocoele; qp, queue post-anale; s, stomocorde; sbr, sac branchial; sca, sinus cardiaque; se, septum; sqp, squelette du proboscis; vsd, vaisseau sanguin dorsal; vsv, vaisseau sanguin ventral.

1.3 SYSTÉMATIQUE

Les entéropneustes sont l'une des quatre classes d'organismes deutérostomiens

faisant partie du phylum des hémicordés (Hemichordata): Enteropneusta, Pterobranchia, Planktosphaeroidea, Graptolithina (éteint). Jusqu'à présent, 78 espèces appartenant à 14 genres et 5 familles ont été identifiées à travers le monde, incluant 17 espèces en Amérique du Nord. Les cinq familles actuellement reconnues sont les Harrimaniidae Spengel, 1901, les Ptychoderidae Spengel, 1893, les Spengelidae Willey, 1897, les Saxipendiidae Woodwick & Sensenbaugh, 1985 et les Torquaratoridae Holland *et al.*, 2005. La famille des Harrimaniidae compte présentement les 5 genres suivants: *Saccoglossus* Schimkewitsch, 1892, *Harrimania* Spengel, 1893, *Stereobalanus* Spengel, 1901, *Xenopleura* Gilchrist, 1925 et *Protoglossus* van der Horst, 1939.

Nos connaissances actuelles sur les entéropneustes ne reflètent toutefois pas la diversité réelle du groupe. En raison de leur mode de vie endobenthique, les entéropneustes font partie de la faune marine qui passe souvent inaperçue et leur grande fragilité fait en sorte qu'on prélève rarement des spécimens intacts. Leur étude est donc beaucoup plus ardue que pour la majorité des autres invertébrés marins. De ce fait, le nombre réel d'espèces et leur distribution demeurent inconnus. Sur les côtes nord-américaines, de nombreuses populations n'ont jamais été étudiées.

Les entéropneustes sont un groupe relativement homogène d'animaux qui possèdent très peu de caractères uniques permettant de distinguer les différents genres et espèces. Il existe en plus une grande confusion dans la nomenclature des caractères utilisés pour la classification des espèces, certains termes provenant de descriptions anciennes souvent librement traduites de l'allemand, d'après les travaux de Spengel (1893, 1901). Comme plusieurs espèces ont été décrites à partir de spécimens uniques, de nombreux états de caractères ne sont pas connus pour l'ensemble des espèces et rendent la classification d'autant plus incertaine. Chacun des auteurs ayant basé sa description sur des suites de caractères anatomiques différents, accordant plus d'importance à certains et ignorant d'autres, nous nous retrouvons en présence de descriptions taxonomiques difficilement comparables les unes aux autres. De surcroît, comme plusieurs de ces espèces n'ont été trouvées qu'une seule fois et que les spécimens les plus communs sont souvent rares et fragiles, il est difficile de vérifier à nouveau la

présence des caractères ignorés.

Quelques ouvrages généraux sont toutefois disponibles sur la biologie et l'anatomie du groupe, dont les plus importants sont ceux de Hyman (*The Invertebrates*, 1959), Dawydoff (*Traité de zoologie*, 1948) et Horst (*Bronn's Klassen und Ordnungen des Tierreichs*, 1939). Le traité taxonomique le plus complet étant celui de Horst (1939), écrit en allemand et aujourd'hui malheureusement désuet, un nouvel ouvrage taxonomique sur les enteropneustes s'avère nécessaire pour une meilleure compréhension du groupe, que ce soit simplement pour l'uniformisation de la nomenclature des caractères. C'est seulement en examinant de nombreux spécimens qu'on pourra déterminer quels sont les caractères taxonomiques stables et utiles. Ayant accès à la collection de Ritter et Bullock, nous espérons être en mesure de clarifier, du moins en partie, la validité des caractères au sein de la famille.

1.4 DONNÉES HISTORIQUES INÉDITES

En participant à l'expédition Harriman de 1899 en Alaska, William E. Ritter avait accumulé une collection considérable de spécimens d'entéropneustes provenant de la côte est du Pacifique et avait commencé, au début du siècle dernier, la rédaction d'un travail taxonomique sur ces nouvelles espèces. Les descriptions de deux espèces furent publiées séparément (Ritter 1900, Ritter & Davis 1904), mais l'ouvrage complet ne fut jamais terminé. En 1937, T. H. Bullock héritait du projet et ajoutait de nouveaux spécimens à la collection. Il confia plus tard le projet à K. P. Rao, puis à C. Burdon-Jones, mais malgré leur contribution la monographie ne vit jamais le jour. En 2004, Bullock confia finalement le manuscrit à Christopher Cameron en souhaitant qu'il puisse être complété.

Le présent mémoire est donc la suite d'un projet de longue haleine, bien connu des zoologistes de la côte ouest et parfois cité par les auteurs d'ouvrages importants sur la famille (Hyman, 1959 et Ricketts *et al.*, 1985). Dans le présent travail, six espèces de

cette collection appartenant à la famille Harrimaniidae sont décrites et ajoutées aux quatre espèces de la famille présentement connues pour la côte ouest de l'Amérique du Nord, soit *Saccoglossus pusillus* (Ritter & Davis, 1904), *Saccoglossus bromophenolosus* (King, Giray, & Kornfield, 1994), *Harrimania maculosa* (Ritter, 1900) et *Harrimania planktophilus* (Cameron, 2002). Bien que la majorité des espèces ici traitées soient peu répandues ou représentées par un seul spécimen, plusieurs d'entre elles semblent communes localement. Il est d'ailleurs fort probable que certaines populations soient déjà connues des zoologistes et qu'on puisse rencontrer ces espèces le long des côtes, sans que l'on sache les identifier.

C'est pour cette raison qu'une description des spécimens découverts jusqu'à présent s'avère plus que nécessaire, puisque l'on sait désormais que les quatre espèces de la famille auparavant décrites pour cette côte ne sont pas représentatives de la richesse spécifique de cette région.

1.5 CONTRIBUTION DES DIFFÉRENTS AUTEURS

Les spécimens de la collection furent prélevés par de nombreux zoologistes au cours du 20^{e} siècle et les coupes histologiques furent effectuées par plusieurs techniciens dans le laboratoire de T. H. Bullock. Les descriptions originales de *Mesoglossus intermedius* gen. et sp. nov. et de *Horstia kincaidi* gen. et sp. nov. furent élaborées par Ritter. Rao effectua une première révision des descriptions de Ritter et rédigea les descriptions originales de *M. macginitiei* gen. et sp. nov. et de *Ritteria ambigua* gen. et sp. nov.. Finalement, j'ai préparé moi-même la description de *Protoglossus mackiei* sp. nov. par l'observation de spécimens de la collection de Bullock.

De plus, j'ai effectué la révision et l'uniformisation de chacune des descriptions, j'ai ajouté de nouveaux caractères pour chacune des espèces, et j'ai ajouté des planches et figures illustrant l'anatomie des spécimens. J'ai rédigé une nouvelle description de l'espèce

Saxipendium coronatum à l'aide de la documentation et des coupes histologiques de l'holotype, en utilisant la même suite de caractères que celle que j'ai utilisée pour les autres espèces décrites dans ce travail. J'ai aussi illustré les détails de l'anatomie de cette espèce à l'aide d'une nouvelle planche photographique. Finalement, j'ai construit un arbre phylogénétique, une table de caractères, ainsi qu'une clé d'identification à partir de données obtenues de la documentation pour les espèces pour lesquelles nous n'avions pas accès aux holotypes et à partir des coupes histologiques pour les espèces décrites dans ce travail.

2. L'ancêtre deutérostomien et la génétique moderne

L'origine de l'intérêt porté à la classe des enteropneustes est liée aux théories évolutionnaires et provient de la suggestion faite par Bateson (1885) selon laquelle ces animaux seraient des cordés et représenteraient le parent le plus primitif des vertébrés. Le nom Hemichordata fut d'ailleurs proposé par Bateson pour refléter le fait que les hémicordés partagent certaines caractéristiques morphologiques avec les cordés, telles les fentes pharyngiennes, un tube neural dorsal et la stomocorde, une structure ressemblant à la notocorde. Toutefois, l'hypothèse de l'inclusion des hémicordés au sein des cordés fut très contestée, entre autres par les auteurs de trois ouvrages zoologiques importants portant sur cette classe, soit Spengel (1893), Horst (1939) et Dawydoff (1948).

Une étape clé ayant récemment ravivé l'intérêt porté aux entéropneustes provient de l'étude moléculaire de Turbeville *et al.* (1994) qui confirma la monophylie des Ambulacraires (Hemichordata + Echinodermata) et leur position en tant que groupe frère des cordés. Depuis, plusieurs autres études moléculaires et morphologiques ont confirmé la position phylogénétique du groupe (Cameron *et al.* 2000, Swalla *et al.* 2000, Winchell *et al.* 2002, Cameron 2005, Zeng & Swalla 2005, Bourlat *et al.* 2006). Plusieurs des résultats de ces analyses phylogénétiques suggèrent la possibilité que l'ancêtre deutérostomien aurait été un ver semblable aux entéropneustes actuels, ayant des fentes pharyngiennes supportées par un squelette de collagène acellulaire (Cameron *et al.* 2000, Swalla *et al.* 2000, Zeng & Swalla 2005). Ces résultats font en sorte que les entéropneustes jouissent à nouveau d'une certaine popularité dans les domaines de la phylogénétique et de l'évolution. Néanmoins, plusieurs questions demeurent sans réponse au sujet de la nature des caractères deutérostomiens ancestraux. La réponse à ces questions réside, entre autres, dans la distribution des caractères homologues à l'intérieur des divers groupes d'animaux deutérostomiens, et plus particulièrement au sein des entéropneustes (Ruppert, 2005). Comme les entéropneustes sont plus près des échinodermes qu'ils ne le sont des cordés, tout caractère homologue partagé par les deux groupes pourrait avoir été un attribut du dernier ancêtre commun. En fait, au moins deux caractères anatomiques des entéropneustes seraient homologues de ceux des cordés: les fentes branchiales et la queue post-anale (ventrale chez ce groupe, mais considérée

homologue par l'expression des gènes Hox) (Lowe *et al.*, 2003). Les entéropneustes recèlent peut-être même davantage d'homologies, mais malgré le rôle central qu'ils occupent dans les hypothèses sur l'évolution des deutérostomiens, leur anatomie n'a été que peu étudiée depuis les travaux de Horst (1939), Bullock (1945), Rao (1954) et plus récemment Cameron (2005). En raison de ce manque d'information, on sait d'ailleurs très peu de choses sur l'évolution des caractères morphologiques au sein même du groupe et par conséquent, sur la systématique des divers genres et familles.

Les études moléculaires et morphologiques récentes ayant tenté de clarifier les relations au sein des entéropneustes ont mené à l'élaboration d'hypothèses contradictoires concernant la position des familles et même en ce qui a trait aux classes du phylum Hemichordata. Les données provenant de l'analyse morphologique (Cameron, 2005) indiquent que les entéropneustes sont un groupe monophylétique, plaçant les ptérobranches à la base des hémicordés. Elles démontrent aussi la monophylie des familles Spengelidae et Ptychoderidae, mais ne présentent aucune résolution quant aux autres familles dont les membres ont une anatomie plus simple. Une analyse de l'ADNr 28s (Winchell *et al*., 2002) démontre la monophylie des entéropneustes en plaçant les ptérobranches comme groupe frère des entéropneustes, mais ne clarifie pas la systématique des familles en raison d'un jeu de données trop limité. Finalement, diverses études basées sur les séquences d'ADNr 18s démontrent que les entéropneustes sont un groupe paraphylétique et placent les ptérobranches en tant que groupe frère de la famille Harrimaniidae (Cameron *et al.* 2000, Bourlat *et al.* 2003, Cannon *et al.* 2009).

Si la dernière hypothèse s'avère exacte et que les ptérobranches ont évolué à partir de vers entéropneustes, l'étude de la morphologie de ces derniers devient d'autant plus importante pour la découverte des caractères deutérostomiens ancestraux, puisque les entéropneustes posséderaient un plan corporel moins dérivé que celui des ptérobranches.

3. Objectifs du travail

L'objectif premier de ce mémoire est de faire la description anatomique de spécimens appartenant à de nouvelles espèces de la famille des Harrimaniidae provenant de populations de la côte ouest de l'Amérique du Nord, dans une perspective de classification taxonomique. À l'aide d'une collection de coupes histologiques de spécimens amassée au cours du siècle dernier, d'abord par W. E. Ritter et T. H. Bullock, puis par K. P. Rao, nous avons pu ajouter cinq nouvelles espèces et trois nouveaux genres à la famille Harrimaniidae, en plus de faire la description d'une espèce découverte par Ritter, qui n'avait pas encore été véritablement décrite. Nous avons aussi tranféré l'espèce *Saxipendium coronatum* dans cette famille et en avons fait une nouvelle description.

Ayant eu l'opportunité de travailler sur ce qui est probablement la collection d'entéropneustes la plus importante au monde quant au nombre de spécimens et d'espèces, l'objectif second de ce projet est de réviser la taxonomie de la famille Harrimaniidae en vérifiant d'abord, à l'aide des spécimens disponibles, les caractères morphologiques déjà décrits dans la documentation, et ensuite d'établir des listes de caractères pertinents pour la classification.

4. Article: A taxonomic revision of the family Harrimaniidae (Hemichordata: Enteropneusta) with descriptions of seven species from the Eastern Pacific

Accord des coauteurs

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Titre: A taxonomic revision of the family Harrimaniidae (Hemichordata: Enteropneusta) with descriptions of seven species from the Eastern Pacific

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Déclaration de tous les coauteurs autres que l'étudiant

À titre de coauteur de l'article identifié ci-dessus, je suis d'accord pour que Carine Deland inclue cet article dans son mémoire de maîtrise qui a pour titre **Révision taxonomique de la famille des Harrimaniidae (Hemichordata: Enteropneusta) incluant les descriptions de sept espèces de la côte Est du Pacifique**

Christopher B. Cameron

Coauteur Signature Date

ABSTRACT

The family Harrimaniidae of the enteropneust hemichordates is revised on the basis of morphological characters. The number of harrimaniid genera is increased to nine by the addition of *Horstia* n. gen., *Mesoglossus* n. gen., *Ritteria* n. gen and *Saxipendium,* a genus previously assigned to the monospecific family Saxipendidae. The number of species is increased to thirty-four, resulting from the description of five new species from the eastern Pacific: *Horstia kincaidi, Mesoglossus intermedius*, *Mesoglossus macginitiei*, *Protoglossus mackiei* and *Ritteria ambigua*. A description is supplied for a sixth harrimaniid species, *Stereobalanus willeyi* (Ritter and Davis, 1904), which previously had the status of a *nomen nudum*. Four harrimaniids previously assigned to the genus *Saccoglossus* are transfered to the genus *Mesoglossus*: *M. bournei*, *M. caraibicus*, *M. gurneyi,* and *M. pygmaeus*, while *Saccoglossus borealis* is reassigned to the genus *Harrimania*. Notes on habitat and zoogeography are included for the seven foregoing species, a table of diagnostic characters for old and new species and a dichotomous key for the enteropneust families and harrimaniid genera are provided. Finally, a phylogenetic hypothesis to the Harrimaniidae is postulated with discussion on the evolution of the group.

Key Words: acorn worm, zoogeography, *Xenopleura*, dichotomous key, phylogeny

INTRODUCTION

The family Harrimaniidae is one of the five families of enteropneusts. Of the 79 enteropneust species known to date, 28 are classified in this family, which consists at the time of writing of the following five genera: *Harrimania*, *Protoglossus*, *Saccoglossus*, *Stereobalanus* and *Xenopleura*. Members of this family include common and widely distributed North American species such as *Saccoglossus kowalevskii* (Agassiz, 1873) and *Saccoglossus pusillus* (Ritter, 1902). Found in all latitudes, from the intertidal zone to the deep sea, enteropneusts inhabit sand or mud, occasionally under rocks or among seaweed holdfasts. Typical habitats are clean coral sand flats exposed at low tides and black mud under clean sea water. Some species may be located by a coiled casting of sand thrown up in a cone at one end of the burrow. But most species are encountered only by chance digging in the right place.

Our work is based in part on an unpublished manuscript and specimen collection initiated a century ago by William E. Ritter and later continued by Theodore H. Bullock and Kandula P. Rao. Our present study incorporates a part of this unpublished material to revise and update the family Harrimaniidae, to which we add five new species and three new genera. In addition, a description is provided for *Stereobalanus willeyi*, heretofore a nomen nudum. Moreover, an expanded description is provided for *Saxipnedium coronatum* (Woodwick and Sensenbaugh, 1985) and these findings coupled with recent molecular phylogenetic results (Cannon *et al.*, 2009) indicate that the monospecific genus *Saxipendium* should be transferred to the Harimaniidae. From the older unpublished material plus our own contributions, we synthesize a new generic classification within the family.

Our morphological descriptions of haramaniid genera and species is incorporated into a dichotomous key as well as a table listing the characteristic features of each species of the family. It is hoped that our textural material along with the photographic plates and generic relationships will make the work more accessible to non-specialists.

THE SPECIMEN COLLECTION

As an outgrowth of his extensive studies on tunicates, Ritter took up the subject of the Enteropneusta in the last decade of the nineteenth century and published several accounts dealing with natural history, embryology and taxonomy (Ritter, 1900; Ritter, 1902; Ritter, 1908; Ritter & Davis, 1904). Over a period of years he accumulated a considerable body of material, representing seven new species from the west coast of the United States and Alaska. He obtained many of his specimens during the Harriman Alaska Expedition of 1899, the results of which appeared in a series of volumes (C. Hart Merriam, ed., Harriman Alaska Expedition, 13 volumes. New York: Doubleday, Page and Company, Washington, D.C.: Smithsonian Institution, 1901-1914). The then recent summary by Spengel (1893) of the enteropneusts of the world listed no species from this coast so that Ritter, with a proportionately considerable new fauna relative to the forty or so species known for the entire group at that time projected a monograph, and put into draft descriptions and figures of all these forms. Descriptions of two of the species were later published separately (Ritter, 1900; Ritter & Davis, 1904), but the full monograph was never completed.

Shortly before he died in 1944, Professor Ritter gave his enteropneust slides and manuscript to Theodore H. Bullock, who had recently finished a doctoral dissertation on the neuroanatomy of the group (Bullock, 1940, 1944, 1945). Bullock subsequently undertook to update and complete the paper, with the aid of Kandula Pampapathi Rao who had previously studied the group extensively (Rao, 1952, 1953, 1954, 1955, 1957, 1962). They then found new material in the Albatross collection through the kindness of C.A. Kofoid and S.F. Light, both of the Department of Zoology, University of California, Berkeley and in the collections at the Scripps Institution of Oceanography, through the courtesy of Percy Barnhart. In the ensuing years Bullock found a number of additional new eastern Pacific species, as well as receiving valuable specimens from others.

C. Burdon-Jones inherited the task of completing the monograph in the early seventies but had not made any significant contribution to the work. In 2003 Bullock, then well into his retirement years, urged that Burdon-Jones, then at a later age and in poor health, return what material he had to California so that the whole collection could be deposited at the Smithsonian Museum in Washington. Bullock feeling a deep obligation to see the monograph complete then contacted Cameron, who had developed a graduate thesis on the group, including the description of a new species (Cameron, 2002a), to complete the work. Following the death of Bullock in 2005, Cameron decided that it would be most practical to publish the new material as several smaller papers instead of as a comprehensive monograph.

DIAGNOSTIC MORPHOLOGICAL CHARACTERS

Species (and even genera and families) of enteropneust hemichordates differ mainly in their unique combinations of morphological features and presence or absence of soft parts, traced in serial sections. Not many features are by themselves diagnostic. These features are only to a limited degree established, from examination of many individuals of abundant species, to be consistent characters. Even less is known of variation that might be due to seasonal, ontogenetic, local environmental factors and the like. In general, only single or very few specimens are examined for all relevant characters, both because of the rarity of finds and because of the formidable labor of serial sectioning and interpreting sizable, sandy, coiled worms. The paucity of hard parts and the distortions of soft parts in fixation add to the problems.

The net result is almost certain to be that some of the characters used are not good species characters and we do not place undue weight on the validity of the taxa named. Nevertheless the characters have a certain modicum of reliability to judge from the few species repeatedly examined and are sanctified by usage. Until better characters, e.g. molecular and other biochemical signatures are validated, we perforce deal with these.

We have faced the same dilemma as previous authors, namely, whether to risk confusion by ignoring morphological differences that have not been well shown to be significant or to risk confusion by paying attention to them, in short whether to lump or split. Our decision, after some years of dealing with this group in various respects, is that the lesser evil is to split. Especially when such a high percentage of the published species are represented by unique specimens or part of a specimen, errors uncovered in the future will be easier to correct by throwing names into synonymy than the reverse. This has already happened in the widespread and abundant species of *Ptychodera,* of which only two are now recognized. We have been particularly conscious of the possibility that this may be called for in multispecific genera like *Saccoglossus* and *Mesoglossus*.

In the present state of understanding there is no justification for collapsing harrimaniid species into synonymy, even with the substantial number of sectioned specimens we were able to examine. The resulting bulk of material and number of species at hand is quite likely to be considerably in excess of any assembly of material that has been available to any previous author. This certainly does not mean that we have arrived at greater insight into evaluation of characters or regard our taxa as more likely to last. It does correlate with a serious concern, a long hesitancy to perpetrate new genera and species and a decision to do so only after fairly protracted efforts.

MATERIAL AND METHODS

The specimens used in this study are part of T. H. Bullock's enteropneust slides collection deposited at the Smithsonian Institution National Museum of Natural History, Washington, DC. Most of the material in this collection has been fixed in Bouin's solution, while some of it was fixed in formol-acetic-alcohol and all the material has been archived by transfer to 80% alcohol with 10% glycerin. Sections were cut either

in paraffin or in low viscosity nitrocellulose and mounted on glass slides. Heidenhain's iron alum haematoxylin, Masson's trichrome or Mallory's triple stain were used for staining the sections. Specimens were viewed and photographed with a Q Imaging Retiga-2000R digital camera mounted on an Olympus BX51 compound microscope and on an Olympus SZX16 stereomicroscope for lower magnifications.

Being soft and fragile enteropneusts are usually taken as pieces. These are nevertheless valuable. Whatever enteropneust material is collected should be carried back to the laboratory in separate containers since the chances of their suffering damage, if mixed with hard shells or hard skinned marine organisms, is very great. They should be preserved soon after collection. Good preservation is most desirable as all serious study depends upon serial sectioning and histologic staining. It is quite desirable to leave them in a tray of clean sea water for a few hours to allow evacuation of the sand from the gut; frequent removal of the sand and the mucous sheath with its sand grains may avoid reingestion. Fixation without coiling is aided if each worm is lifted into the air by a match stick under the middle of the specimen and killed by dropping fixative solution over it for a few minutes. It may then be lowered into the fixative. A general histologic fixative such as Bouin's, Hedenhain's Susa fluid, formol-acetic-alcohol or 10% formalin is satisfactory. Changing the fluid twice in the first 24 hours and again after several days is more than desirable. Labels should give not only details of the geographic locality, date of collections and name and address of collector, but also of the nature of substratum, color of the body parts in life and method of preservation. A sketch or photograph with measurements in life showing length and diameter of different regions is helpful.

RESULTS

SYSTEMATIC DIAGNOSES OF FAMILY AND GENERA

CLASS ENTEROPNEUSTA Gegenbaur, 1870

FAMILY HARRIMANIIDAE Spengel, 1901

Balanoglossidae Willey, 1899

Enteropneusta characterized by the absence of circular muscle fibers in the trunk. In those cases where the development has been studied, the typical tornaria larva is absent and the development is direct. In addition to these two unique features may be added the following characters: absence of lateral septa, absence of vermiform process of the stomochord, absence of hepatic caeca in the trunk and absence of synapticulae joining the primary and secondary gill bars (for a drawing of a generalized enteropneust, see Fig. 1 from Cameron, 2005). The dorsal nerve roots in the collar mesentery and the intestinal pores may be present or absent. The skeletal cornua extend at least to the middle of the collar.

Of the five known genera included in this family, *Harrimania*, *Saccoglossus*, *Protoglossus*, *Stereobalanus* and *Xenopleura*, the first two occur in the Eastern Pacific. In addition, as a result of the present work, *Protoglossus* and *Stereobalanus* genera can now be added to this list, along with the three new genera described here (*Ritteria*, *Horstia* and *Mesoglossus*) and *Saxipendium,* which is transferred to the family Harrimanidae, effectively eliminating the monospecific family Saxipendidae.

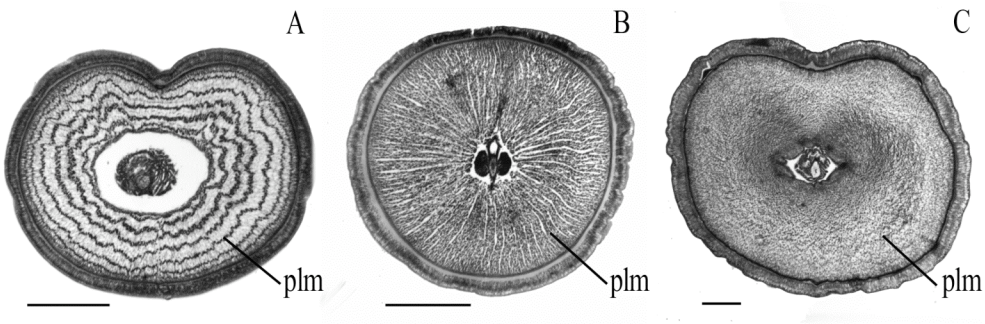

Figure 2.1 Light micrographs of transverse sections of the proboscis of (A) *Saccoglosus pusillus,* showing the arrangement of the proboscis longitudinal musculature in concentric rings; (B) *Protoglossus mackiei* n. sp., showing the arrangement of the proboscis longitudinal musculature in radial plates; (C) *Mesoglossus macginitiei* n. gen. and sp., showing the diffuse arrangement of the proboscis longitudinal musculature. plm, proboscis longitudinal muscles. Scale bars = 500 µm.

Genus *Saccoglossus* Schimkewitsch, 1892

Dolichoglossus Spengel, 1893

Type species: *Saccoglossus kowalevskii* (Agassiz, 1873)

The proboscis is usually long; a middorsal longitudinal groove may be present. The collar is usually very short compared to the proboscis. Dorsal inter-branchial genital ridges and dorsal gonads are absent, but lateral extra-branchial genital ridges may be present. Intestinal pores are often present. Perihaemal cavities are always present. Peribuccal cavities are usually present, but not always. More important than all the above characters, the genus is characterized by the arrangement of the longitudinal muscle fibers of the proboscis in several concentric rings (Fig. 2.1 A). Many species favor quiet flats not too far from the mouth of a bay, in muddy sand; live in "permanent" tubes and throw up low conical mounds of quasi-spiral castings from the anus.

The genus as revised above would now include the following species: *S. apatensis* (Thomas, 1956), *S. aulakoeis* (Thomas, 1968), *S. bromophenolosus* (King, Giray & Kornfield, 1994), *S. horsti* (Brambell & Goodhart, 1941), *S. hwangtauensis* (Tchang & Koo, 1935), *S. inhacensis* (Kapelus, 1936), *S. kowalevskii* (Agassiz, 1873), *S. madrasensis* (Rao, 1957), *S. mereschkowskii* (Wagner, 1885), *S. otagoensis* (Benham,

1895), *S. pusillus* (Ritter, 1902), *S. ruber* (Tattersall, 1905), *S. sulcatus* (Spengel, 1893) and five new species collected from the Eastern Pacific which will be described in a forthcoming article on the genus.

Genus *Harrimania* Spengel, 1893

Type species: *Harrimania kupfferi* (von Willemoes-Suhm, 1871)

The proboscis is conical and a little longer than broad; the collar is broader than long. The longitudinal muscles of the proboscis are arranged in radial plates (Fig. 2.1 B). The genus is often characterized by two proboscis pores. Intestinal pores and peribuccal cavities are absent. In *H. maculosa* (Ritter, 1900) and *H. planktophilus* (Cameron, 2002a), the cornua are very long and extend into the trunk. They also form parabuccal ridges on either side of the buccal cavity in the collar. Both dorsal and lateral gonads can be present and occur as simple sacs arranged in long rows. The dorsal gonads, when present, are confined to the branchial region.

Three species from this genus are currently described, two of which are from the Eastern Pacific region: *H. maculosa* and *H. planktophilus*. From the description given above, we should now reassign *Saccoglossus borealis* (Okuda & Yamada, 1955) to this genus, for its great resemblance to *H. planktophilus* in its possession of a radial proboscis musculature, a broad collar, a left proboscis pore, lateral gonads, parabuccal ridges and the absence of peribuccal cavities.

Genus *Stereobalanus* Spengel, 1901

Balanoglossus Spengel, 1893

Type species: *Stereobalanus canadensis* (Spengel, 1893)

The genus is characterized by broad dorsolateral and ventrolateral genital ridges, with the broad gill opening situated in between. The gill tongues are externally visible.

The longitudinal musculature of the proboscis is arranged in radial plates. Abdominal pores may or may not be present. Perihaemal cavities are present but the peribuccal coelomic cavities are absent. The genus possesses two proboscis pores, but they are greatly reduced. Contrarily to the report of Spengel (1893), collar ducts are present in this genus (Reinhard, 1942).

Two species, namely, *S. canadensis* and *S. willeyi* are included in this genus and both are represented on the west coast of North America.

Genus *Xenopleura* Gilchrist, 1925

Type species: *Xenopleura vivipara* Gilchrist, 1925

The genus is characterized by the presence of medullary folds in the trunk extending posteriorly on the dorsal side into low pleurae. The proboscis is not elongate, and its longitudinal muscles are scattered (Fig. 2.1 C). The stomochord is without a vermiform process, and is continuous through the buccal cavity as two dorso-lateral folds. There is one proboscis pore. The posterior margin of the collar is fused with the trunk and no nerve roots are present in the collar nerve cord. The branchial skeleton lacks synapticula, and internal hepatic caeca are present in the trunk. This genus, only described from one specimen, could be viviparous.

Genus *Protoglossus* van der Horst, 1939

Balanocephalus Caullery & Mesnil, 1900*; Protobalanus* Caullery & Mesnil, 1904

Types species: *Protoglossus koehleri* (Caullery & Mesnil, 1900)

This genus is characterized by a short conical proboscis with a deep posterior dorsal groove and a conspicuous horseshoe-shaped pre-oral ciliary organ. The longitudinal musculature of the proboscis is radial. Its paired dorsal gonads are not prominent. It is also considered as having the simplest arrangement of body cavities of

all enteropneusts in not possessing peribuccal cavities and having rudimentary or no perihaemal cavities (Burdon-Jones, 1956). A left proboscis pore is present as are dorsal and ventral mesenteries in the proboscis and collar. The cornua of the skeleton extend to the posterior margin of the collar forming parabuccal ridges on each side of the buccal cavity.

Genus *Saxipendium* Woodwick & Sensenbaugh, 1985

Type species: *Saxipendium coronatum* Woodwick & Sensenbaugh, 1985

This genus, previously assigned to its own family is here transferred to the family Harrimaniidae. It possesses the general characters of the family and can be distinguished from the other genera of the family by the following characters: diffuse longitudinal proboscis mucles, coronate body of the proboscis skeleton, absence of skeleton keel, long recurved skeletal cornua, collar canals with pores opening to the outside of the body, dorso-lateral genital ridges with the gonopores externally visible and the possible presence of testicular antra.

Genus *Mesoglossus* gen. nov.

Type species: *Mesoglossus bournei* (Menon, 1904)
Saccoglossus bournei Menon, 1904

The genus has the following features distinguishing it from other genera of Harrimaniidae. The proboscis, about twice as long as wide, has no conspicuous dorsal groove. Its longitudinal musculature is arranged diffusely, not in concentric rings or radial bundles. A proboscis pore is present usually on the left side. Perihaemal cavities are usually present. Collar canals are present. A ventral mesentery is present in the proboscis and both dorsal and ventral mesenteries are present in the collar. Dorsal gonads are absent, only the lateral gonads are present. Peribuccal spaces may be present or absent.

It is evident from the details given above that the closest relations of this species are four species previously assigned to the genus *Saccoglossus* but here transferred to the genus – namely, *Mesoglossus*: *M. bournei*, *M. caraibicus* (van der Horst, 1924), *M. gurneyi* (Robinson, 1927), and *M. pygmaeus* (Hinrichs & Jacobi, 1938). Although all these species and *M. intermedius* resemble species of *Saccoglossus* a great deal, they are distinguished from the latter by the fact that the longitudinal muscle fibers of the proboscis are uniformly distributed without being arranged into concentric rings as in *Saccoglossus* (or into radial groups as in *Harrimania* and *Stereobalanus*). *Mesoglossus* is too distinct to be confused with *Stereobalanus*. Hence all the forms which have previously been put under *Saccoglossus* but which exhibit no regular arrangement of the proboscis longitudinal muscle fibers into concentric rings are here transferred to the genus *Mesoglossus*, with *M. bournei* as the type species.

Remarks: The description given above is primarily based on Ritter's account in his manuscript of circa 1900 and a re-examination of his own slides and of material collected by others. At the beginning of the twentieth century, no *Saccoglossus* species had been described with a diffuse distribution of longitudinal fibers in the proboscis, except for Benham's description of *S. otagoensis* (Benham, 1895). But it is now known that in *S. otagoensis* the longitudinal muscle fibers in the proboscis are actually arranged in 3 or 4 concentric rings (van der Horst, 1939). Thus *S. otagoensis* cannot be considered as belonging to *Mesoglossus*, which means that *M. bournei* is the earliest described species under the genus and should be considered as its type species.

Genus *Ritteria* gen. nov.

Type species: *Ritteria ambigua* gen. & sp. nov.

Created for the single species *R. ambigua*, the genus conforms to the diagnosis of the family and may be defined tentatively by the following selection of characters of the type species. The proboscis is short and its longitudinal muscles are dispersed diffusely, not concentrically or radially. There is a single, left proboscis pore. The proboscis neck

is severely reduced and the stomochord lumen broken into lacunae. There is neither dorsal nor ventral septum in the collar and no peribuccal cavities. Dorsal gonads are present and, with the lateral gonads forming two pairs of genital ridges, leaving the branchial pores recessed in the groove between them.

The genus is named in honor of Professor W.E. Ritter, but for whose interest and initiative our knowledge of the enteropneusts would have been very much poorer. He never saw the material on which this name is based so that we are not deterred by his insistent modesty.

Genus *Horstia* gen. nov.

Type species: *Horstia kincaidi* gen. & sp. nov.

Having the characters of the family, this genus is distinguished from others of the Harrimaniidae by the following combination of features. The proboscis is very short and round, hardly as long as broad. Its longitudinal muscles are arranged in radial plates. A proboscis pore is present on the right or the left. An anterior neuropore is present and there are large lacunae in the collar nerve cord. Peribuccal cavities are absent. The gonads do not form ridges; the cross section of the trunk is regular and nearly circular with the gill pores unusually prominent, even elevated a bit above the general surface level. There are no dorsal gonads. The gonads are conspicuous as modules projecting prominently from the surface. Thus *Horstia* differs in at least three or four characters from the nearest genera (*Mesoglossus*, *Saccoglossus*, *Harrimania* and *Ritteria*) and currently comprises only one species (*H. kincaidi*), which would otherwise have to be forced into one of these genera, doing violence to what we believe are defining generic features. *Horstia* is of course only tentatively defined by the foregoing selection of characters of its single species; further discoveries may reveal some of generic rank in the specific description below.

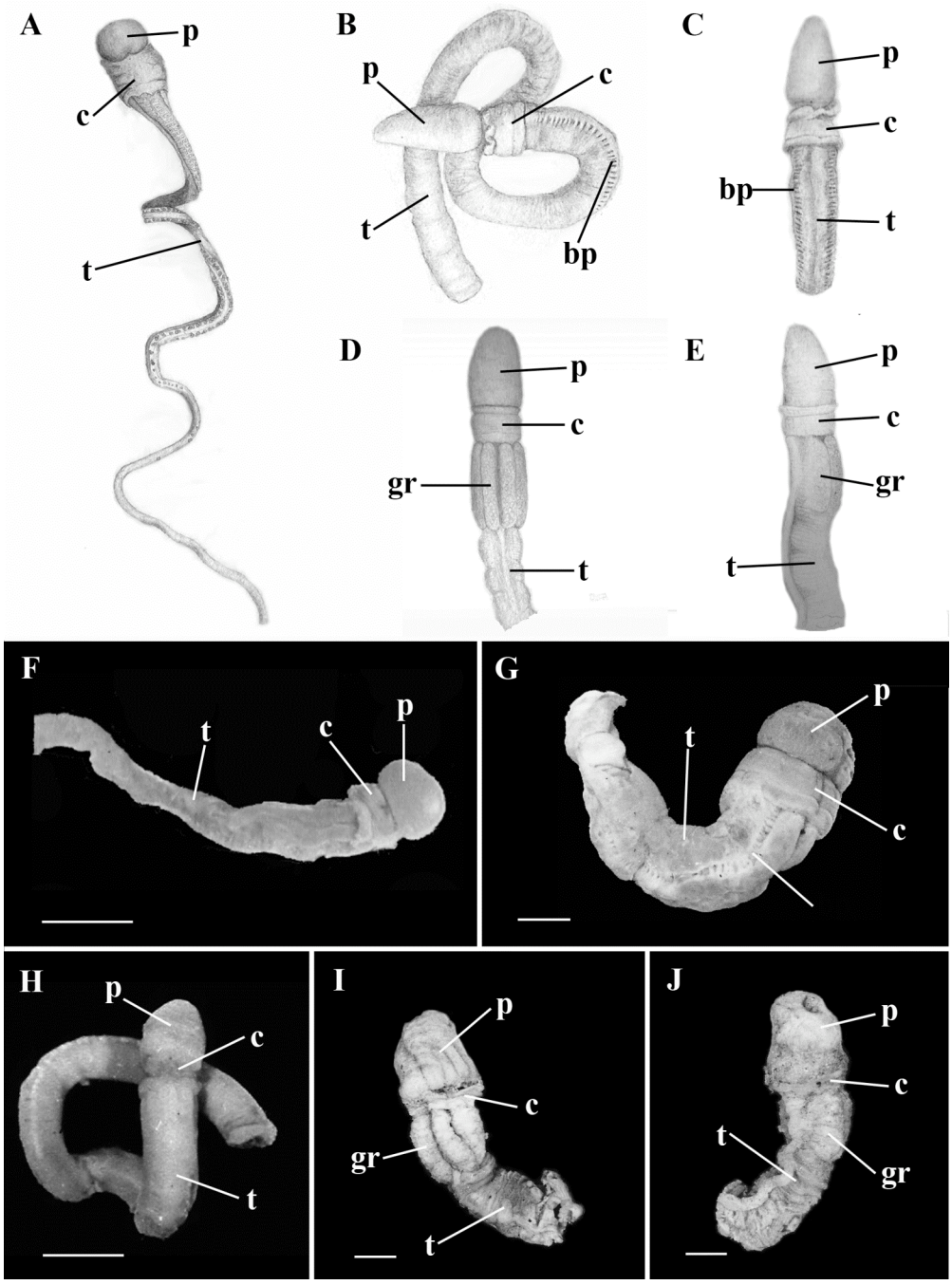

Figure 2.2 Drawings of live animals and photographs of fixed specimens of the family Harrimaniidae. (A) Drawing of the dorsal side of *Horstia kincaidi* n. gen. and sp.. (B) Drawing of the lateral side of *Mesoglossus intermedius* n. gen and sp.. (C) Drawing of the dorsal side of *Mesoglossus intermedius*. (D) Drawing of the dorsal side of *Stereobalanus willeyi* n. sp.. (E) Drawing of the lateral side of *Stereobalanus willeyi.* (F) Photograph of the dorsal side of *Horstia kincaidi*. (G) Photograph of the lateral side of *Ritteria ambigua* n. gen. and sp.. (H) Photograph of the dorsal side of *Mesoglossus intermedius*. (I) Photograph of the dorsal side of *Stereobalanus willeyi.* (J) Photograph of the lateral side of *Stereobalanus willey*. bp, branchial pore; c, collar; gr, genital ridge; p, proboscis; t, trunk. Scale bars = 2 mm.

SPECIES DESCRIPTIONS

Stereobalanus willeyi sp. nov.

Stereobalanus willeyi Ritter & Davis, 1904: *nomen nodum*

Three anterior fragments were collected around 1900 by Ritter by dredging extremely soft, sandy mud at a depth of about 80 meters in San Pedro Channel, off the coast near Newport, Orange County, California. Accession no. NMNH 71441 is the holotype and Bullock 129 is the paratype.

External features (Fig. 2.2 D, E, I, J)**:** The proboscis is conical, cylindrical in section and about 1 cm long. The collar is less than half the length of the proboscis and rather broader than long, with an expanded rim at the anterior edge. The four genital ridges are distinct and column-like and confined to the branchial region. The branchio-genital region is slightly longer than the proboscis. A prominent ventral keel is seen in the abdominal region. The proboscis is cream color, the collar the same but somewhat lighter. Gonads in the female are bright yellow. The pharyngeal region, excepting the gonads, is nearly the same color as the collar; the abdomen is nearly black; gills as seen from dorsal side when gonads are pressed asunder, appear black.

Internal features (Fig. 2.3)**:** The circular muscle layer of the proboscis is well developed and somewhat thicker than the nerve fiber layer of the ectoderm. Longitudinal muscle fibers are in well defined radial plates (Fig. 2.3 A), particularly toward the base of the proboscis. The stomochord is in the form of a tube without a ventral caecum and with a thick and even wall (Fig. 2.3 B). The stomochordal neck is completely obliterated and no trace of it is found in the neck. The stomochordal sheath is extremely thick. The glomerulus is very limited in development and much scattered, arising as two irregular masses from the dorsal side of the stomochordal sheath (Fig. 2.3 A). The proboscis cavity is obliterated by musculature and glomerulus posteriorly. The cardiac vesicle is rudimentary and has no bifid tip. Proboscis vesicles with canals and pores, one on each side, are reduced to a mere trace. There certainly appears to be some communication

between the proboscis coelom and the proboscis pore through the vesicles and canals, which are all rudimentary. The proboscis skeleton is also much reduced, with no keel and a small piece which is obtrusely rounded anteriorly and continues posteriorly into the cornua (Fig. 2.3 C, D). The cornua arise from the posterolateral margins of the skeletal body and hence are widely separated from each other from their start. They extend to the posterior margin of the collar.

The dorsal nerve cord of the collar is without any dorsal roots. The lumen of the cord is distinct in about its posterior third but not so in the rest of its length. The collar canals and pores are absent. A peribuccal coelom is not present. Perihaemal cavities are conspicuous and extend into the neck. A large posteriorly directed caecum is given off from the ventral side of the buccal cavity in the collar region. This begins anteriorly, a short distance behind the mouth as a broad deep trough which becomes more and more set off by the approximation of the lateral walls of the buccal cavity above it, until finally the walls close together producing a well defined ventral caecum in the middle region of the collar (Fig. 2.3 D). The walls of this caecum are of practically the same histological structure as that of the buccal epithelium immediately adjacent to it.

There are about seventy branchial aperatures on each side and no synapticulae. Parabranchial ridges are prominent (Fig. 2.3 E). Branchial openings are large exposing the gill-tongues to view. Ova are rather large being about 0.5 mm in diameter. There is a pair of lateral and a pair of dorsal genital ridges starting immediately behind the collar. There is a single pair of intestinal pores in the abdominal region.

This species is clearly more closely related to *S. canadensis* (Spengel, 1893), than to any other known species. It is sharply distinguished from *S. canadensis* by its color, the possession of a much larger number of branchial pores, the shape of the proboscis skeleton, the complete absence of the collar canals and pores, the caecum on the ventral side of the buccal cavity and the possession of intestinal pores.

In his manuscript account Ritter says this of the derivation of the specific name: "I take great pleasure in dedicating this interesting form to Dr. Arthur Willey in whose extensive contributions to the Zoology of the South Pacific, the Enteropneusta had a liberal share."

The above description of *S. willeyi* is mainly based on the manuscript of Ritter. Ritter and Davis (1904) listed this species by name as one whose description was forthcoming, mentioning that it has two proboscis pores and could not be the parent of a tornaria larva they were studying. This being inadequate as an indication, the species cannot be regarded as having heretofore been published. The living authors of the present paper have examined the sections critically and have brought a few changes in the description given by Ritter. The references to this name given in the synonymy clearly refer to the same specimens although no adequate indication is provided with which the species could be recognized. The type specimen is accession no. 71441.

The defining characters of *Stereobalanus willeyi* are listed below:

A. Proboscis conical, longer than broad
B. No proboscis groove
C. Longitudinal musculature of the proboscis is in radial plates
D. Two minute proboscis pores on either sides of the dorsal midline
E. Proboscis skeleton has no keel
F. Posterior neuropore
G. No peribuccal diverticula in the collar
H. No collar canals
I. 4 columnar genital ridges confined to the gill region
J. 1 pair of esophageal pores

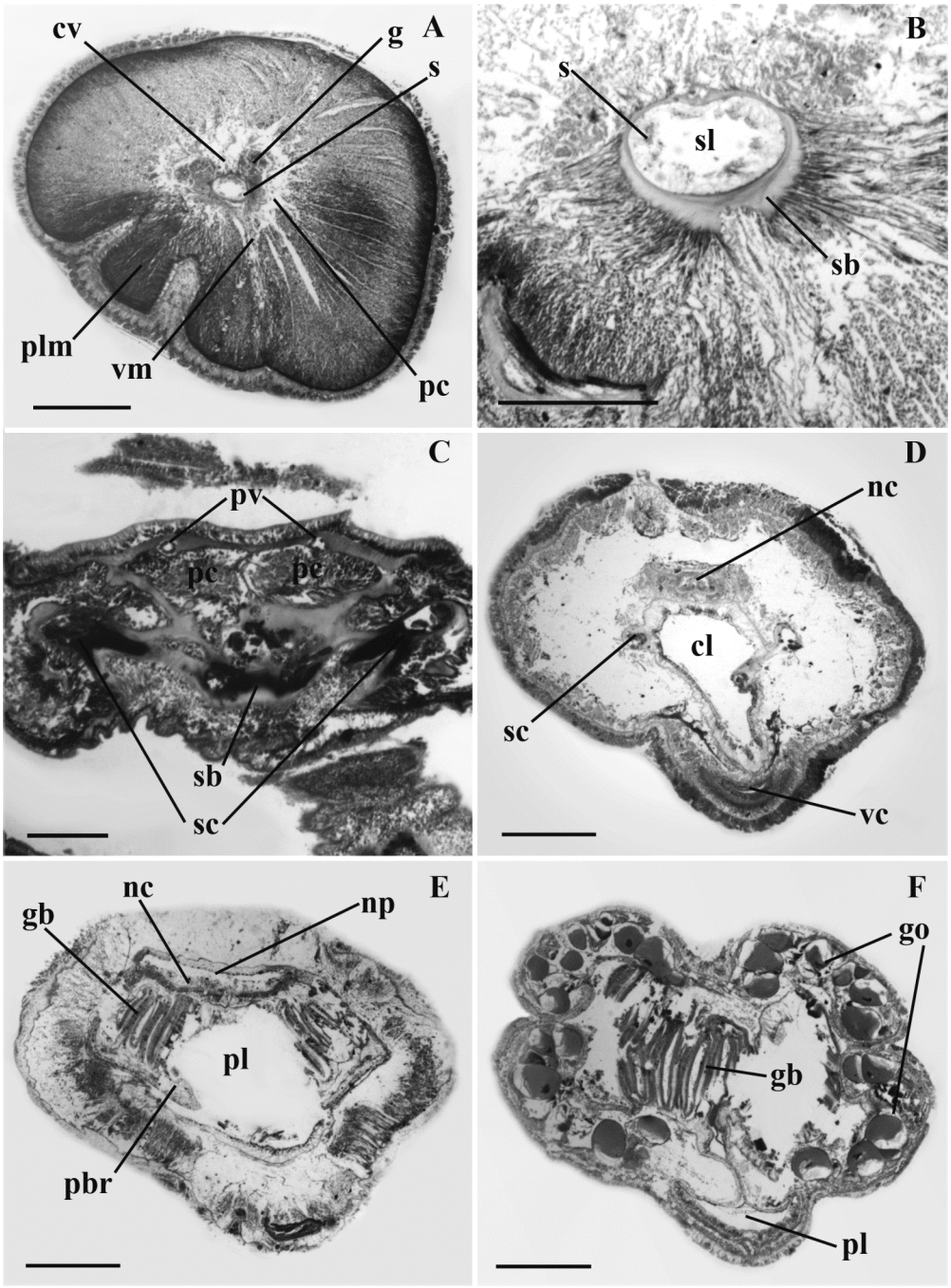

Figure 2.3 Light micrographs of transverse sections of *Stereobalanus willeyi* n. sp.. (A) Proboscis with heart-kidney complex. (B) Posterior part of the proboscis showing the skeleton. (C) Proboscis neck. (D) Anterior region of the collar. (E) Anterior pharyngeal region of the trunk. (F) Genital region of the trunk. cl, collar lumen; cv, cardiac vesicle; g, glomerulus; gb, gill bar; go, gonad; nc, nerve cord; np, neuropore; pbr, parabranchial ridge; pc, proboscis coelom; pl, pharynx lumen; plm, proboscis longitudinal muscles; pv, proboscis vesicle; s, stomochord; sb, skeletal body; sc, skeletal cornua; sl, stomochord lumen; vc, ventral caecum; vm, ventral mesentery. Scale bars (A, D, E and F) = 1000 µm; (B) = 500 µm; (C) = 750 µm.

Protoglossus mackiei sp. nov.

Three complete specimens were collected by Theodore H. Bullock at Moss Beach, San Mateo, California (37° 52' N, 122° 52' W) on May 22nd 1939. The holotype is accession number NMNH 71493. They have been found under surface of rocks, resting in coarse sand and were not in tubes or holes.

External features: The shape of the proboscis of preserved specimens is conical, not short or round. The collar is broader than long and has a ruffled anterior border and a dark central area. The length of preserved specimens is 25 mm and they are about 2 mm thick. In live material, the collar is yellow and the proboscis and trunk are white.

Internal features (Fig. 2.4)**:** The nerve fiber layer of the proboscis is thickened mid-dorsally (Fig. 4 A). The proboscis coelom extends to the tip of the organ as a narrow cavity closely surrounding the proboscis complex. The ventral and dorsal septa are present and start along with the proboscis complex. They are both continuous throughout the length of the organ. The circular muscle fiber layer is thinner than the nerve fiber layer. The longitudinal muscle fibers are arranged in radial plates, but are not as well defined as in *Horstia*. The small glomerulus extends over the tip of the stomochord as two small lateral wing-shaped projections (Fig. 2.4 A, A inset). The cardiac vesicle is well developed and only covers the dorsal side of the stomochord (Fig. 2.4 A, A inset). The stomochord has thick walls and a continuous narrow lumen that gives off a single small ventral diverticulum, anterior to the pore, where the skeletal plate is forming. The proboscis has a deep dorsal groove posteriorly. The skeleton has a well developed acute keel (Fig. 2.4 B, C). The two coelomic cavities in the neck are present and there is also one conspicuous left vesicle leading to the exterior by a left proboscis pore (Fig. 2.4 B).

Both the dorsal and ventral mesenteries of the collar are complete. The perihaemal diverticula start at the level of the proboscis pore and are separate throughout their length (Fig. 2.4 C). The peribuccal coeloms are absent. The skeletal cornua extend

to the posterior margin of the collar and are confined to the dorso-lateral aspect (Fig. 2.4 D). The cornua project into the lateral walls of the buccal cavity forming two dorso-lateral evaginations, or parabuccal ridges, along their length. The collar canals are well developed and horizontal (Fig. 2.4 E, E inset). Two lacunae are often present in the dorsal nerve cord (Fig. 2.4 D inset), one on each side, but are not continuous throughout the whole length of the cord. There is a small anterior neuropore (Fig. 2.4 C) and the posterior one may or may not be present. The collar longitudinal muscles are well developed and are present as two irregular masses on each side of the collar lumen (Fig. 2.4 D, E).

The branchial portion of the pharynx is equal in size to the ventral portion or slightly larger (Fig. 2.4 F). There is a pair of dorso-lateral gonads, but they are not prominent on the surface of the body. Well developed branchial sacs open by dorso-lateral pores. The presence of intestinal pores could not be determined. The ventro-lateral longitudinal muscles of the trunk are well developed but do not form ridges.

We dedicate this animal for Professor George O. Mackie of the University of Victoria who has extensively contributed to our understanding of the form and function of invertebrates of the Pacific Coast of North America.

The defining characters of *Protoglossus mackiei* are listed below:

A. The proboscis is conical with a deep posterior dorsal groove
B. The longitudinal musculature of the proboscis is in radiating plates
C. The dorsal and ventral mesenteries are present in the proboscis and collar but the ventral mesentery is absent in the trunk
D. The perihaemal diverticula are present and start in the neck
E. The peribuccal diverticula are absent
F. There is an anterior neuropore
G. There are parabuccal ridges in the collar on either side of the buccal cavity
H. The collar canals are well developed and horizontal
I. The two rows of lateral gonads do not form ridges

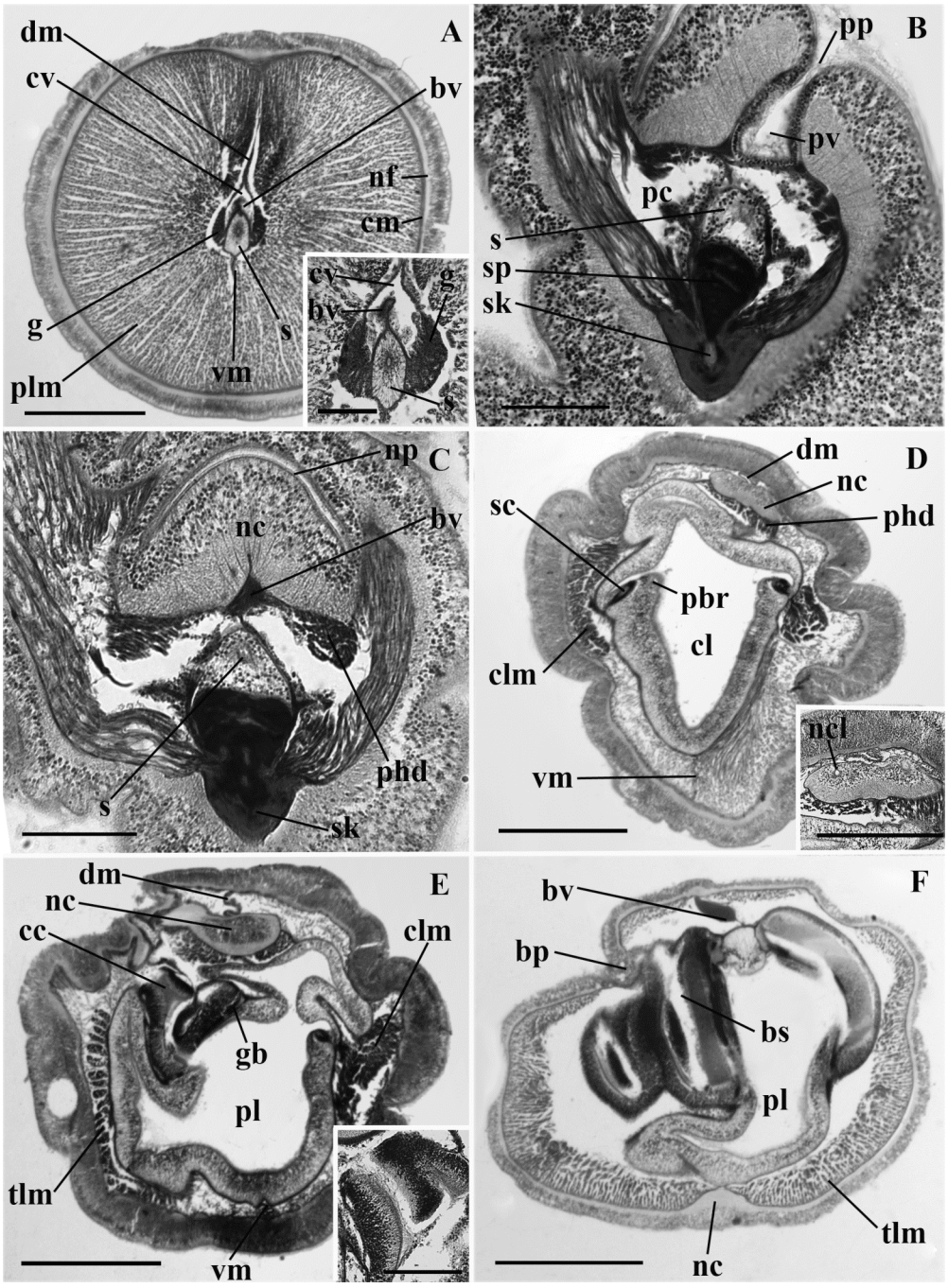

Figure 2.4 Light micrographs of transverse sections of *Protoglossus mackiei* n. sp.. (A) Proboscis with heart-kidney complex. (A inset) Proboscis complex. (B) Proboscis neck. (C) Proboscis neck showing the neuropore. (D) Collar, (inset) collar nerve cord. (E) Anterior pharyngeal region of the trunk, (inset) collar canal. (F) Pharyngeal region of the trunk. bp, branchial pore; bs, branchial sac; bv, blood vessel; cc, collar canal; clm, collar longitudinal muscles; cm, circular muscle layer; cv, cardiac vesicle; dm, dorsal mesentery; g, glomerulus; gb, gill bar; nc, nerve cord; ncl, nerve cord lacunae; nf, nerve fiber layer; np, neuropore; pbr, parabuccal ridge; pc, proboscis coelom; pl, pharynx lumen; plm, proboscis longitudinal muscles; phd, perihaemal diverticulum; pp, proboscis pore; pv, proboscis vesicle; s, stomochord, sc, skeletal cornua; sk, skeletal keel; sp, skeletal plate; tlm, trunk longitudinal muscles; vm, ventral mesentery. Scale bars (A, E, G and I) = 500 µm; (B, C, D and H) = 100 µm; (F) = 300 µm.

Saxipendium coronatum Woodwick & Sesenbaugh, 1985

Eleven specimens were collected by the deep diving submersible Alvin in 1979 near "Rose Garden" geothermal vent, Galapagos Rift (00° 47.9' N, 86° 13.5' W), 2478 m depth. The holotype is NMNH 97395 and paratypes are 97396-8. They have been found loosely attached to the rocks located at the periphery of the vent area.

External features: The proboscis is arrow shaped, longer than broad and has a longitudinal dorsal groove. The collar is very short with an elevated ring at its posterior end. The trunk is slightly flatten dorso-ventrally and presents a median longitudinal groove. There are dorso-lateral genital ridges on each side of the body, with the gonopores externally visible. The length of preserved specimens is 25 mm and they are about 2 mm thick. In live material, the color is yellow-white with the collar darker than the rest of the body and the collar ring paler. The holotype had the following measurements: overall length 215 mm, poroscis 11.0 mm, collar 3.0 mm, trunk 201 mm.

Internal features (Fig. 2.5)**:** The nerve fiber layer of the proboscis is thickened dorsally (Fig. 2.5 A). The proboscis coelom occupies the posterior third of the proboscis. The ventral septum is present in the posterior part of the organ, but the dorsal one is formed by the large cardiac vesicle, which is in contact with the dorsal wall of the proboscis (Fig. 2.5 A). The circular muscle fiber layer is half the thickness of the nerve fiber layer. The longitudinal muscle fibers are diffuse. The glomerulus extends over the tip of the stomochord but is poorly developed (Fig. 2.5 A). The stomochord has thick walls with a large central lumen. In the neck region, the stomochord expands ventro-laterally to form two horns, each with its own lumen (Fig. 2.5 B). The two coelomic cavities in the neck are present and a left vesicle leads to the exterior by a left proboscis pore (Fig. 2.5 B). The skeletal body starts in the neck, forming a crown-shaped plate, with the spikes dividing the stomochord into subsections (Fig. 2.5 C). The skeleton has no keel. The proboscis has a dorsal groove, which is more conspicuous on preserved specimens.

Only the dorsal mesentery of the collar is present. There is an anterior neuropore forming at the level where the dorsal part of the collar fuses with the neck (Fig. 2.5 C). The perihaemal diverticula start at the level of the cornua and are fused in some specimens (Fig. 2.5 D). The peribuccal diverticula are absent. The skeletal cornua extend to near the end of the collar (Fig. 2.5 D, E). They bend ventrally around the gut and then bend back anteriorly for a short portion (Fig. 2.5 G). The collar longitudinal muscles are well developed, and are present as masses on each side of the collar lumen (Fig. 2.5 C, D, E, G). The collar canals present a unique feature, connecting the coelom to the outside through pores located in the dorso-medial (Fig. 2.5 E, F). As in other species, the collar canals also connect to the first gill pouch (Fig. 2.5 G).

The branchial portion of the pharynx is equal in size to the ventral portion or slightly smaller (Fig. 2.5 H). The dorsal and ventral mesenteries are present. The two rows of dorso-lateral gonads form external ridges. The gonads connect to the exterior with externally visible gonopores situated on top of the genital ridges (Fig. 2.5 H). The branchial sacs open by dorso-lateral pores recessed between the genital ridges and the elevated median line of the trunk (Fig. 2.5 H). The type specimen had 54 branchial pores and 40 oesophageal pores. The ventro-lateral longitudinal muscles of the trunk are poorly developed.

Woodwick and Sesenbaugh mentioned the presence of an antrum, a special chamber connecting the testis and the gonopore and thought it to be a distinctive feature of this species. As for now, there is doubt on the uniqueness of this character, because new observations showed that in a single specimen, not all the gonads present this feature, and also because so little information is available on the gonads of other species that we cannot certify its absence from other taxa.

The defining characters of *Saxipendium coronatum* are listed below:

A. The proboscis is arrow shaped with a posterior dorsal groove
B. The longitudinal musculature of the proboscis is diffuse
C. The proboscis skeleton is coronate, without a visible keel

D. The skeletal cornua are recurved
E. The dorsal and ventral mesenteries are present in the trunk, but only the ventral one is present in the proboscis and the dorsal one in the collar
F. The cardiac vesicle is in contact with the dorsal wall of the proboscis
G. The perihaemal diverticula are present and start at the level of the skeletal cornua
H. The peribuccal diverticula are absent
I. There is an anterior neuropore
J. The collar canals open into the first branchial sac and also to the exterior via collar pores
K. The gonads form two dorso-lateral ridges and the gonopores are externally visible

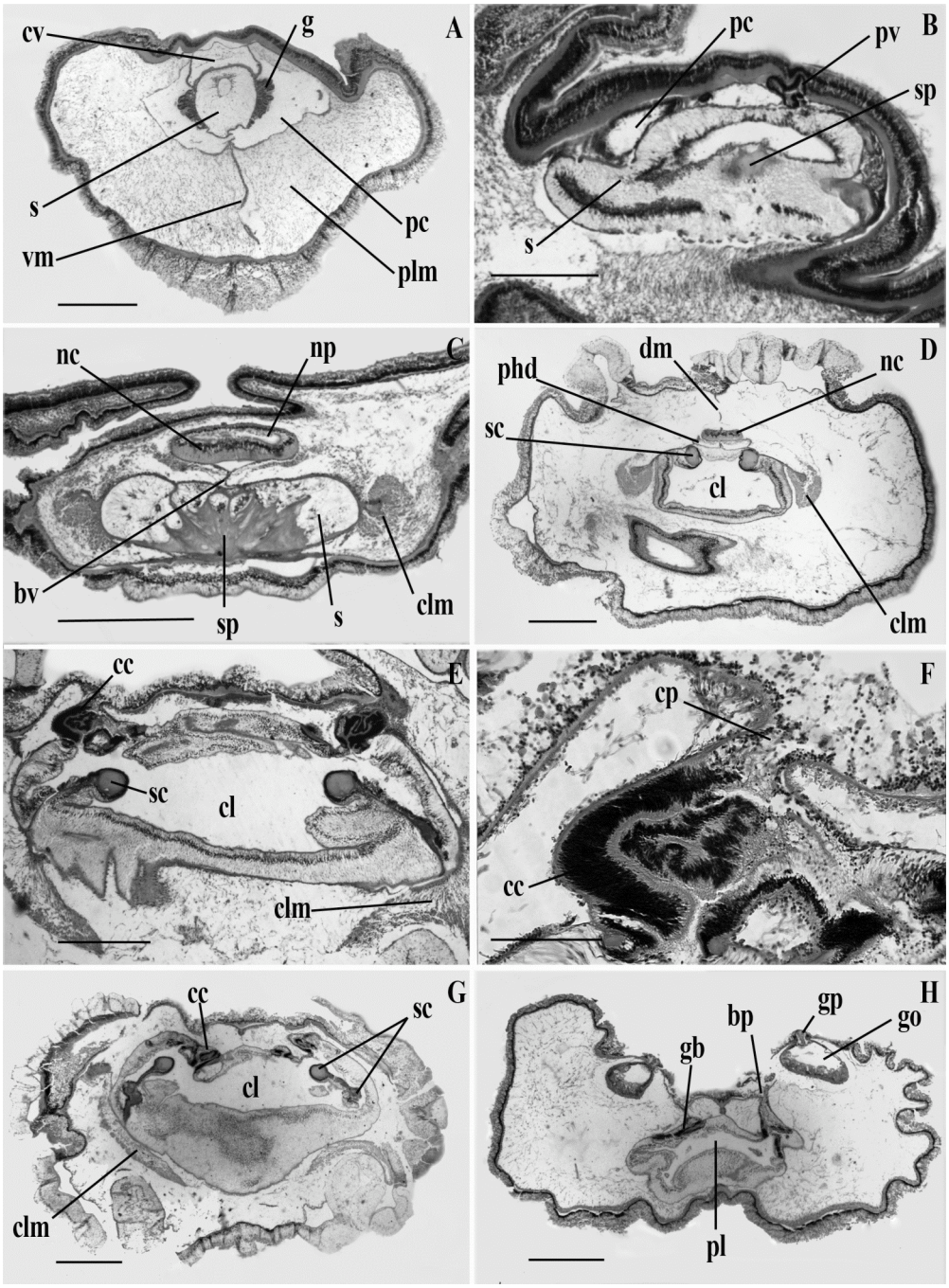

Figure 2.5 Light micrographs of transverse sections of *Saxipendium coronatum*. (A) Proboscis with heart-kidney complex. (B) Anterior region of the proboscis neck. (C) Posterior region of the proboscis neck showing the neuropore and skeleton plate. (D) Anterior region of the collar. (E) Posterior region of the collar showing the collar pores. (F) Collar canal and pore. (G) Posterior region of the collar showing the curved skeletal cornua. (H) Anterior region of the trunk. bp, branchial pore; bv, blood vessel; cc, collar canal; cl, collar lumen; clm, collar longitudinal muscles; cp, collar pore; cv, cardiac vesicle; dm, dorsal mesentery; g, glomerulus; gb, gill bar; go, gonad; gp, gonopre; nc, nerve cord; np, neuropore; pc, proboscis coelom; phd, periheamal diverticulum; pl, pharynx lumen; plm, proboscis longitudinal muscles; pv, proboscis vesicle; s, stomochord; sc, skeletal cornua; sp, skeletal plate; vm, ventral mesentery. Scale bars (A, C, D, G and H) = 1000 µm; (B and E) = 500 µm; (F) = 200 µm.

Mesoglossus intermedius gen. & sp. nov.

A single good specimen and two posterior fragments were taken from a kelp holdfast in Shelter Cover, Humbolt County, California (37° 60' N, 122° 51' W) in 1893 and 1894 by S.J. Holmes; the specimen with the anterior end (NMNH accession no. 71492) will be the type. For decades northern California was entirely barren of further enteropneust finds while southern California yielded a good many. About 40 years later they began to turn up near Moss Beach, San Mateo County and in 1939, with an interested student making frequent trips, more than 20 were found in a few weeks (Bullock accession nos. 145, 203). They occurred typically on the under surface of sizeable rocks resting in coarse, shelly sand, on the protected outer coast, at zero tide level, not in noticeable burrows.

External features (Fig. 2.2 B, C, H)**:** Relaxed living specimens are 25 mm long, but they can extend to 75 mm when crawling. The proboscis is about 2 mm long when relaxed, or only about twice its thickness; it is conical with no trace of a middorsal groove. The length of the collar is about 1 to 1.5 mm or two-thirds of its thickness. Its surface is divided into three regions. The pharynx is less than twice the length of the proboscis. About twenty-five long elliptical branchial orifices occur on either side, situated dorso-laterally. Gonads are invisible in surface view and are extra-branchial only. No external liver lobes are visible. No projecting ventral muscle bands are seen, the body presenting an almost perfectly circular outline in transverse section in all regions. The color in life is light yellow, the proboscis somewhat darker.

Internal features (Fig. 2.6)**:** The circular muscle fiber layer in the proboscis is very thin. Longitudinal muscle fibers are scattered uniformly in the proboscis cavity and are not arranged either in concentric rings or in radial bundles (Fig. 2.6 A). The right and the left halves of the glomerulus join anteriorly over the tip of the stomochord. The glomerulus is rather small and limited and is closely enveloped by the proboscis musculature (Fig. 2.6 A). The cardiac vesicle is rather small (Fig. 2.6 A). The stomochord has thick walls in its anterior part and a narrow lumen (Fig. 2.6 A). The

ventral caecum is single and distinct and is best seen in sagittal sections. The skeleton has a normally developed acute keel (Fig. 2.6 B, C). A well developed ventral septum is present in the base of the proboscis, extending nearly to the tip of the stomochord. No dorsal septum is present. There is a well developed left proboscis vesicle opening by a left proboscis pore (Fig. 2.6 B).

Both the dorsal and ventral mesenteries of the collar are complete (Fig. 2.6 D). Collar musculature is delicate. There is no central lumen nor are there any lacunae in the collar nerve cord. The nerve cord has no dorsal crest and does not give rise to any dorsal roots. There are no epidermal pockets or neuropores either in the anterior or in the posterior face of the collar. The perihaemal diverticula extend anteriorly only up to the commencement of the skeletal cornua (Fig. 2.6 D). There are no peribuccal cavities. The collar canals are short vertical tubes opening along with the first pair of gill pores (Fig. 2.6 E, E inset). The skeletal cornua reach to the posterior margin of the collar.

The branchial part of the pharynx is half the total cross section (Fig. 2.6 F). Branchiae with individual pouches, each opening to the exterior by a pore dorso laterally. Pores of the left and right sides alternate normally, a few here and there being paired or opposite. The ciliated branchial epithelium is thick with nuclei in several strata. Gonads start about 2 mm behind the collar.

The defining characters of *Mesoglossus intermedius* are listed below:

A. Proboscis is conical and longer than broad
B. Longitudinal musculature of the proboscis is scattered
C. No proboscis groove
D. Collar has a ruffled anterior edge and a posterior ring
E. Left proboscis pore
F. The cornua extend to the posterior edge of the collar
G. Ventral proboscis septa
H. Dorsal and ventral collar septa
I. Short vertical collar canals
J. The two of dorso-lateral rows of gonads start 2 mm behind the collar and do not form ridges

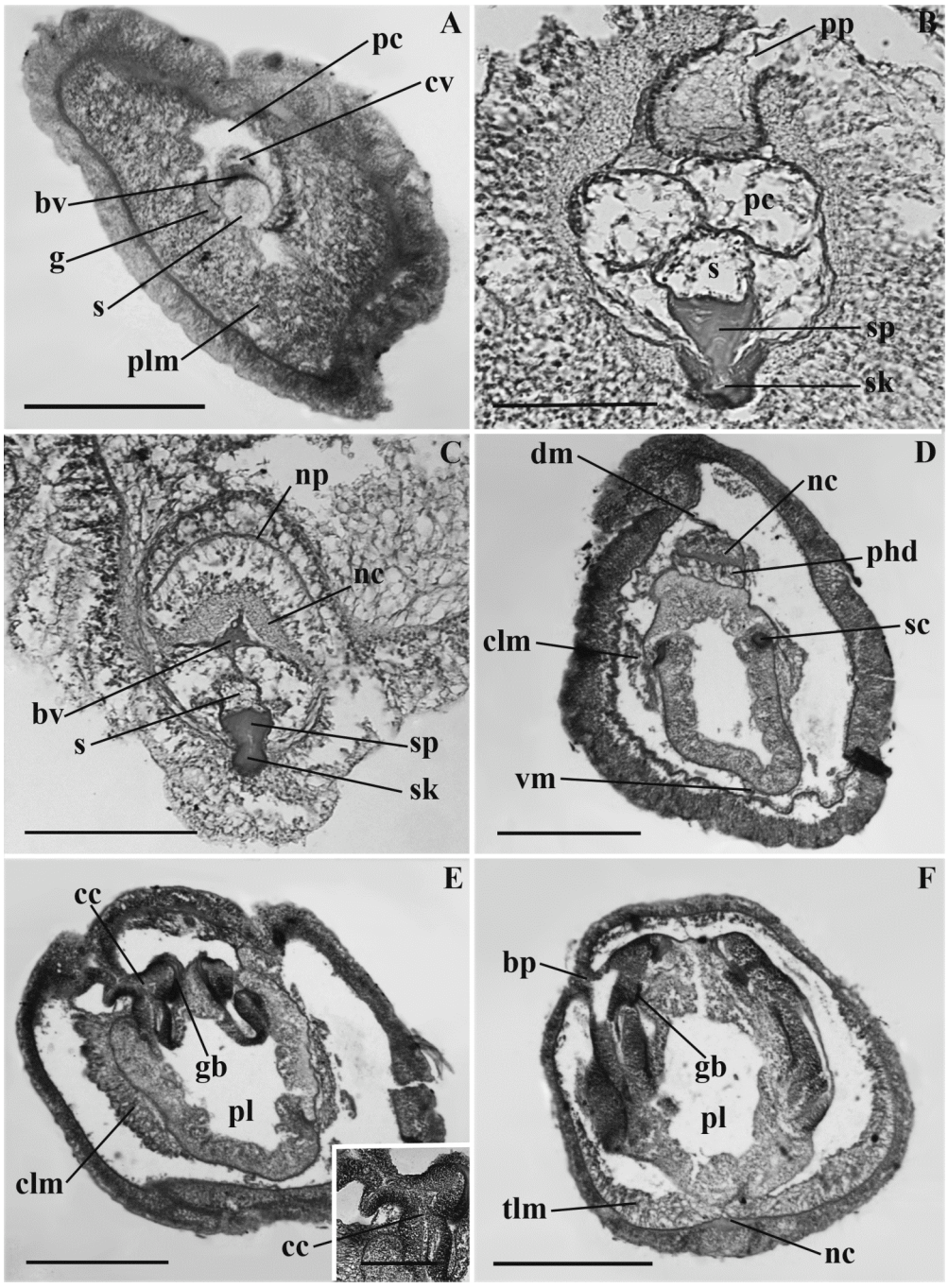

Figure 2.6 Light micrographs of transverse sections of *Mesoglossus intermedius* n. gen. and sp.. (A) Proboscis with heart-kidney complex. (B) Proboscis neck. (C) Proboscis neck showing the neuropore. (D) Collar. (E) Posterior region of the collar, (inset) collar canal. (F) Anterior pharyngeal region of the trunk. bp, branchial pore; bv, blood vessel; cc, collar canal; clm, collar longitudinal muscles; cv, cardiac vesicle; dm, dorsal mesentery; g, glomerulus; gb, gill bar; nc, nerve cord; np, neuropore; pc; proboscis coelom; phd, perihaemal diverticulum; pl, pharynx lumen; plm, proboscis longitudinal muscles; pp, proboscis pore; s, stomochord; sc, skeletal cornua; sk, skeletal keel; sp, skeletal plate; tlm, trunk longitudinal muscles; vm, ventral mesentery. Scale bars (A, D, E and G) = 500 µm; (B) = 100 µm; (C and F) = 200 µm.

Mesoglossus macginitiei gen. & sp. nov.

A single specimen has been collected by Professor G.E. MacGinitie in September 1938, from the intertidal zone in Newport Bay, California, (33° 35' N, 117° 53' W) in sandy mud. The type specimen bears accession no. NMNH 58891.

External features: Little is known about the external features of this form. Genital ridges are present as well as ventral muscular ridges in the trunk.

Internal features (Fig. 2.7)**:** The nerve fiber layer in the proboscis is thickened middorsally. The circular muscle fiber layer is quite well formed, being 5 or 6 fibers in thickness. The proboscis coelom does not extend to the tip of the proboscis. Longitudinal muscle fibers are scattered irregularly in the proboscis (Fig. 2.7 A), not being arranged into either concentric rings or radial groups. Paired dorso lateral blood vessels occur under the proboscis epithelia. The glomerulus is continuous anteriorly over the tip of the stomochord and it also covers the dorsal side of the organ posteriorly. The cardiac vesicle stops short of the stomochord anteriorly. About its middle region, the cardiac vesicle covers the stomochord laterally, also (Fig. 2.7 A). The lumen of the stomochord does not extend to its tip; in the tip a few narrow lacunae are found to represent the cavity. Ventro-lateral blind pouches of the stomochord lumen are well developed and open individually into the primary lumen. The ventral septum of the proboscis extends up to the anterior margin of the ventro-lateral blind pouches of the stomochord. The proboscis coelom is lined by conspicuous amoeboid cells (Fig. 2.7 B) and opens out by a single left proboscis pore. The proboscis vesicle is middorsal (Fig. 2.7 C). The body of the proboscis skeleton has an obtuse middorsal ridge (FIg. 2.7 C). The keel is almost absent in the anterior part of the skeleton, but distinct and deep in the posterior part.

Both the dorsal and the ventral mesenteries of the collar are complete (Fig. 2.7 D, E). The collar nerve cord is without a continuous lumen, but lacunae are present here and there. There is an anterior neuropore. The perihaemal diverticula extend up to the

level of the proboscis vesicle and are confluent anteriorly. The nerve cord has a dorsal crest (Fig. 2.7 E inset). The skeletal cornua extend nearly two-thirds the length of the collar, stopping short of the posterior end of the collar by about 2 mm. Peribuccal cavities are present in the form of triangular extensions, with longitudinal muscle fibers (Fig. 2.7 F). Collar canals are horizontally situated and open into the first pair of branchial sacs (Fig. 2.7 F, G, G inset).

The branchial part of the pharynx is larger than the ventral part (Fig. 2.7 G). Branchial tongue bars do not project into the pharyngeal cavity beyond the primary gill bars. Nuclei of the ciliated branchial epithelium lie in several strata. Neither dorsal nor ventral septa occur in the trunk.

M. macginitiei can easily be distinguished from *M. intermedius* by the presence in the former of the genital and ventral muscular ridges in the trunk, the ventro lateral blind pouches of the stomochord, dorsal glomerulus, less pronounced skeletal keel, median proboscis vesicle, the peribuccal diverticula and the neural crest. Of the other *Mesoglossus* species, the present form resembles *M. caraibicus* in having two stomochordal diverticula and a dorsal glomerulus.

We take pleasure in naming the new species after one of the foremost marine ecologists and naturalists of the west coast, Professor G.E. MacGinitie, long Director of the Corona del Mar Laboratory of the California Institute of Technology, who collected and presented this material.

The defining characters of *Mesoglossus macginitiei* are listed below:

A. Longitudinal musculature of the proboscis is scattered
B. Left proboscis pore
C. Proboscis skeleton bears a dorsal ridge
D. Anterior and posterior neuropores
E. Collar nerve cord with nerve crest
F. Peribuccal diverticula present in the collar
G. Skeleton cornua extend to 2/3 of the collar

H. Ventral septa in the proboscis, dorsal and ventral in the collar and none in the trunk
I. Two rows of dorso-lateral genital ridges starting immediately behind the collar

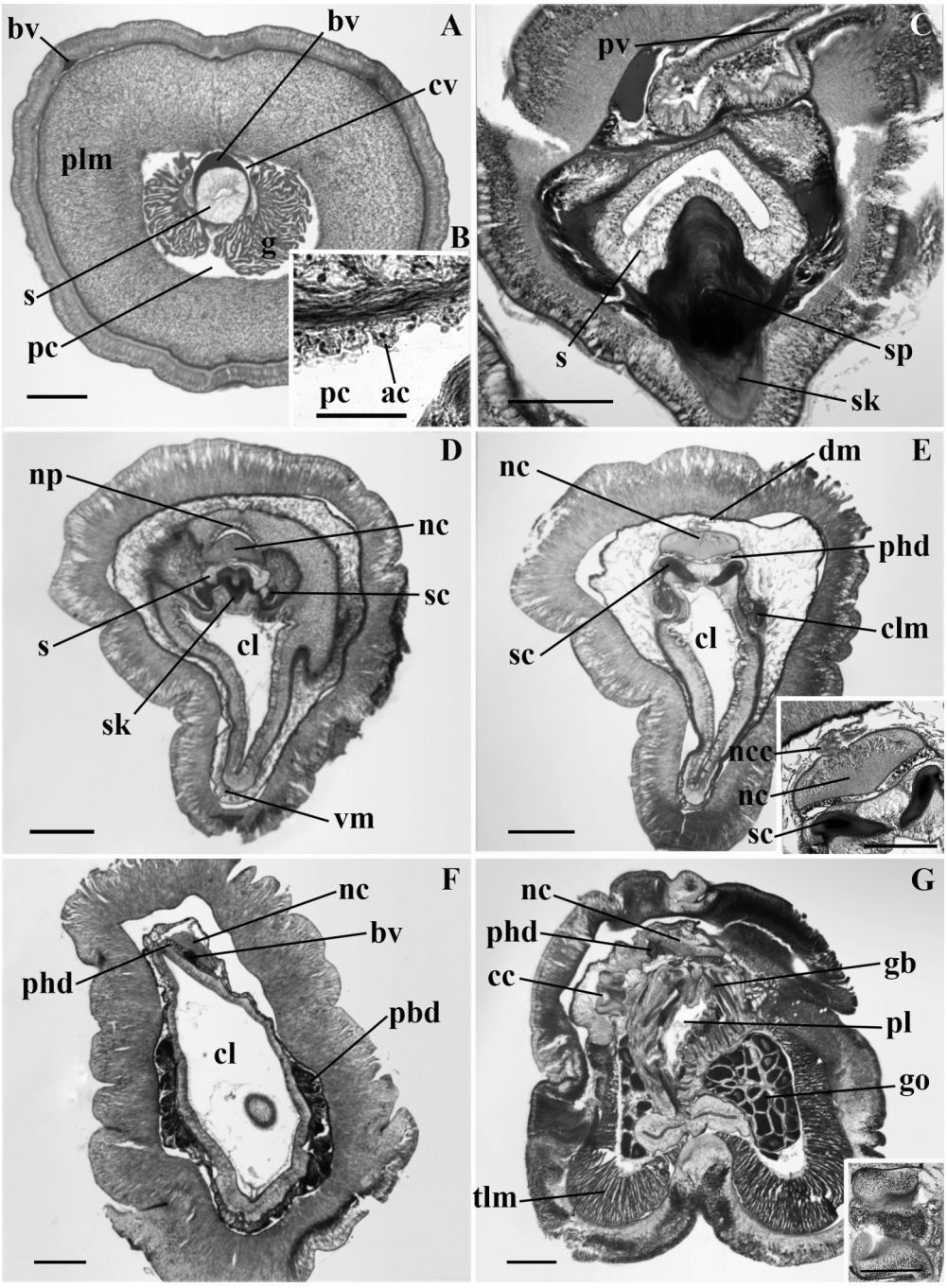

Figure 2.7 Light micrographs of transverse sections of *Mesoglossus macginitiei* n. gen. and sp.. (A) Proboscis with heart-kidney comolex. (B) Proboscis coelomic cavity showing amoeboid-like cells. (C) Proboscis neck. (D) Anterior region of the collar showing the neuropore. (E) Anterior region of the collar showing the dorsal nerve cord crest, (inset) dorsal nerve cord crest. (F) Posterior region of the collar showing the peribuccal diverticula. (G) Anterior pharyngeal region of the trunk, (inset) collar canal. ac, amoeboid-like cells; bv, blood vessel; cc, collar canal; cl, collar lumen; clm, collar longitudinal muscles; cv, cardiac vesicle; dm, dorsal mesentery; g, glomerulus; gb, gill bar; go, gonad; nc, nerve cord; ncc, nerve cord crest; np, neuropore; pbd, peribuccal diverticula; pc, proboscis coelom; phd, perihaemal diverticulum; pl, pharynx lumen; plm, proboscis longitudinal muscles; proboscis vesicle; s, stomochord; sc, skeletal cornua; sk, skeletal keel; sp, skeletal plate; tlm, trunk longitudinal muscles; vm, ventral mesentery. Scale bars (A, D, G and H) = 500 µm; (B) = 50 µm; (C and I) = 200 µm; (F) = 300 µm.

Ritteria ambigua gen. & sp. nov.

A single anterior fragment was collected by Dr. W.K. Fisher at Station 4508 of the Albatross expedition, off Point Pinos, California, (36° 38' N, 121° 56' W), on May 20, 1904, in soft green mud at a depth of 600 to 700 meters. This specimen, accession no. NMNH 58885, becomes the holotype.

External features (Fig. 2.2 G)**:** The total length is unknown. In preserved material from a single specimen the proboscis is short being about 3 mm long and 4 mm wide, the collar is extremely short and broad being about 2 mm long dorsally, 2.7 mm ventrally and its width is about 4.5 mm. The branchial region is between 10-15 mm in length. The collar bears an expanded rim at the posterior edge. Two pairs of genital ridges are present on the dorso-lateral sides, commencing immediately behind the collar, with the gill pores situated along the lateral grooves formed by these ridges. There is a small ventral muscular ridge and hepatic lobes are absent. In living material, the proboscis is coral red, the collar is vermillion deep to poppy red, the posterior margin of the collar and the trunk are bright orange.

Internal features (Fig. 2.8)**:** The circular muscle fiber layer of the proboscis is thinner than the nerve fiber layer, amounting to only 3 or 4 fibers in thickness. The nerve fiber layer is thickened along the mid-dorsal groove into a cord-like structure (Fig. 2.8 A). The longitudinal muscle fibers are neither split into radial bundles nor grouped into circular rings, but are uniformly scattered (Fig. 2.8 A). The proboscis coelomic cavity starts along with the anterior tip of the proboscis complex. The small glomerulus comprises two bilateral masses, which are continuous over the tip of the stomochord. The spacious cardiac vesicle stops shortly before the anterior tip of the proboscis complex (Fig. 2.8 A). The stomochord is large and conspicuous and has a broad lumen at its tip, but there is no lumen throughout its middle region. The ventro-lateral diverticula of its lumen are fused into one, while the lumen in its neck is broken and frequently obliterated. The walls of the stomochord in this region are themselves laminated by strand-like extensions from the body of the skeleton (Fig. 2.8 A), and the

organ here presents the appearance of being broken down into several bits by these strand-like extensions (Fig. 2.8 F). These extensions of collagenous material give the skeletal plate a distinctive coronate form that closely resembles that of *Saxipendium coronatum* (Woodwick & Sensenbaugh, 1985). Just before joining the buccal epithelium, the central part of the neck of the stomochord acquires a distinct lumen. The ventral proboscis septum runs along the midventral line of the stomochord stopping short of its tip and the dorsal septum is absent. The proboscis skeleton is quite massive with a broad and large keel and a wide plate (Fig. 2.8 F). A normally formed left proboscis pore is present and opens into the anterior neuropore by a left vesicle (Fig. 2.8 F).

The collar has neither a dorsal nor a ventral septum. A single dorsal root is seen to emerge from the collar nerve cord in the posterior third of the collar (Fig. 2.8 H). The perihaemal diverticula (Fig. 2.8 C, H) are confined to the collar extending only up to the level of the opening of the stomochord into the buccal cavity. The collar longitudinal muscle are well developed and form triangular bundles on each side of the collar lumen (Fig. 2.8 C). There are no peribuccal diverticula. Collar canals are short and horizontal with a dorsal infolding as in the Ptychoderids (Fig. 2.8 D, G). The skeletal cornua extend to the posterior extremity of the collar but are throughout confined to the dorsolateral aspect (Fig. 2.8 C, D). The ventral longitudinal muscles are poorly developed and do not form bundles nor ridges.

The branchial portion of the pharynx is equal in size to the ventral portion. The gonads are arranged in two pairs of dorso-lateral ridges (Fig. 2.8 E) but do not form wings. The branchial openings are in the form of pores arranged along the groove formed in between the two genital ridges on either side. Consequently, unlike the situation in *Stereobalanus*, the branchial basket is not visible to from the outside. Instead, there are branchial sacs (Fig. 2.8 E) which open out by branchial pores situated dorso-laterally. The ventral longitudinal musculature is forming a small ridge on the ventral surface of the trunk. The presence of intestinal pores could not be determined.

From the above description it can be seen that the species under consideration does not fit into any of the other genera of the family. In the possession of dorsal gonads the present form resembles *Harrimania* and *Stereobalanus*. But those two genera are both characterized by proboscis muscles arranged in radial plates. *Stereoblanus* shares not only the dorsal and lateral gonads but also the apparent degeneration of the neck region of the stomochord. But among other features, the presence of well developed proboscis pore and collar canals are enough to distinguish *Ritteria* from *Stereobalanus*. The differences from other genera are even more numerous.

The resemblances of *Ritteria* to other enteropneusts are rather varied, but as usual in this group, cannot all signify close relationship. We have just referred to similarities between *Ritteria* and *Harrimania* and others between it and *Stereobalanus*. These latter are suggestive of a common trend toward the degeneration of several organs while increasing the emphasis on gonads. Although not conforming to the familial characters, *Ritteria* even resembles the Ptychoderidae in the relatively spacious cardiac vesicle and the extent of the ventral septum of the proboscis. While not putting undue weight on these similarities, by no means unique in this group, we find the situation suggestive of the trivial name *ambigua*.

The defining characters of *Ritteria ambigua* are listed below:

A. Short proboscis and collar
B. Longitudinal musculature of the proboscis is uniformly scattered
C. Proboscis skeleton plate is coronate with extensions of collagen through the stomochord walls
D. Only the ventral mesentery of the proboscis is present (no mesentery in the collar and trunk)
E. Left proboscis pore opening into an anterior neuropore
F. Degeneration of the proboscis neck
G. Presence of a nerve root in the collar nerve cord
H. Well developed horizontal collar canals with a dorsal infolding
I. Two pairs of dorso-lateral genital ridges starting immediately behind the collar

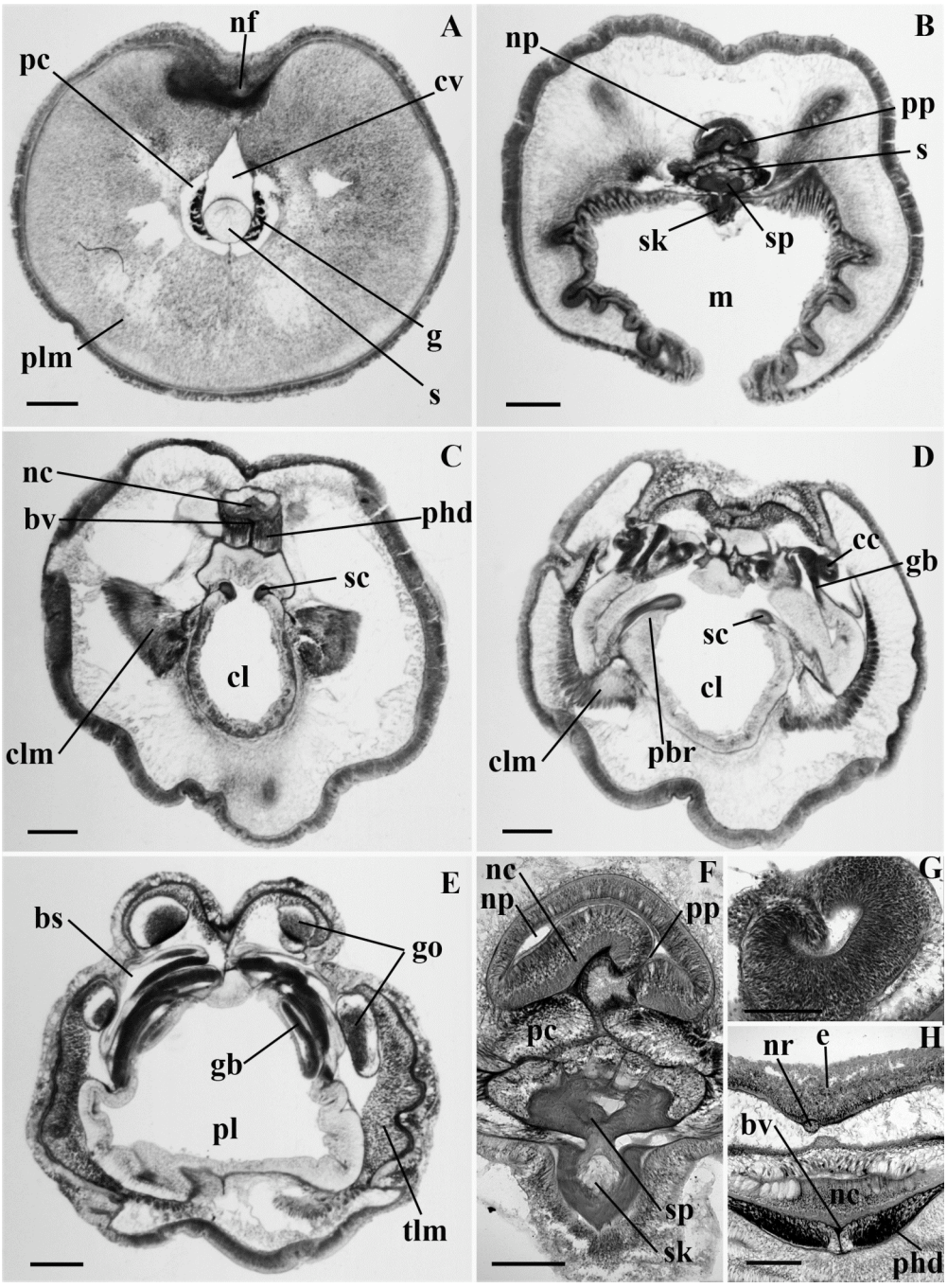

Figure 2.8 Light micrographs of transverse sections of *Ritteria ambigua* n. gen and sp.. (A) Proboscis with heart-kidney complex. (B) Junction of the proboscis and collar. (C) Anterior region of the collar. (D) Anterior pharyngeal region of the trunk. (E) Genital region of the trunk. (F) Proboscis skeleton, neuropore and proboscis pore. (G) collar canal. (H) collar nerve cord showing the nerve root. bs, branchial sac; bv; blood vessel; cc, collar canal; cl, collar lumen; clm, collar longitudinal muscles; cv, cardiac vesicle; e, epithelia; g, glomerulus; gb, gill bar; go, gonad; m, mouth; nc, nerve cord; nf, nerve fiber layer; np, neuropore; nr, nerve root; pbr, parabuccal ridge; pc, proboscis coelom; phd, perihaemal diverticulum; plm, proboscis longitudinal muscles; pp, proboscis pore; s, stomochord; sc, skeletal cornua; sk, skeletal keel; sp, skeletal plate; tlm, trunk longitudinal muscles. Scale bars (A, B, C, D, E) = 500 µm; (F, G, H) = 200 µm.

Horstia kincaidi gen. & sp. nov.

T. Kincaid in 1899 collected a dozen specimens on Whidbey Island in Puget Sound, Washington (47° 59' N, 122° 26' W). It has not been found again. We have both old Ritter and more recent sections made by Bullock of nine of the specimens. Considering the faded condition of the former it seems best to designate one of the latter, Accession no. NMNH 71439 as the holotype; 58879 and Bullock 220 become paratypes.

External features (Fig. 2.2 A, F)**:** The total length is 30-40 mm. The proboscis is 2 mm long, as short as it is wide, the collar is 1.5 - 2 mm long and has irregular surface markings. The branchial region, 6 mm long and tapering to 1.0-1.5 mm wide is exceptionally narrow, and the postbranchial trunk is still more tenuous. Neither genital wings nor hepatic lobes are present. The branchial orifices are conspicuous and their arrangement is distinctive in that the left and right rows are close together on an elevated ridge bounded laterally by a groove. The gonads are also conspicuous as a long series of protruding nodules.

The color in life was said by Professor Kincaid to be brown. In material preserved by Perenyi's fixative the proboscis is a uniform creamy white, the collar and anterior portion of the thorax is only slightly darker. The rest, and most of the length, of the animal is greenish brown with the gonads yellowish white.

Internal features (Fig. 2.9)**:** The longitudinal muscle fibers of the proboscis are arranged in well defined wedge shaped radial plates (Fig. 2.9 A). There is no conspicuous thickening of the nerve fiber layer in the proboscis or any apparent dorsal longitudinal groove. The proboscis coelom extends to the tip of the organ. The glomerulus is poorly developed (Fig. 2.9 A) and limited to two small bilateral masses which are usually well defined in other species, standing out like wings. The pericardial sac is quite spacious, covering the dorsal and lateral sides of the stomochord. The blood vessel is also spacious, almost entirely filling the inside of the pericardial sac (Fig. 2.9

A). Both the ventral and the dorsal mesenteries are present in the proboscis and to the tip of the proboscis complex (Fig. 2.9 A).

The proboscis portion of the stomochord is large and simple, the cavity being clearly defined and with but a slight, posteriorly directed ventral blind lumen. One proboscis pore is present, sometimes to the right and sometimes the left. In one case the coelomic spaces, canals, and terminal vesicles were so nearly symmetrical but for the single pore, that Ritter predicted individuals will be found with both pores.

Peribuccal diverticula are absent. Perihaemal spaces extend forward of the proboscis pore, the cornua of the proboscis skeleton extend nearly back to the posterior edge of the collar and are noteworthy in the steepness and extent of their projection ventral, from their very origin, approaching the transverse plane and nearly reaching the ventral side of the buccal cavity (Fig. 2.9 B). The keel is deep and narrow; there is almost none of the chondroid tissue developed in connection with the body of the skeleton.

The stomochord is continuous through the neck, though narrow. The collar nerve cord has very large lacunae scattered throughout its length. There is a small anterior neuropore and for some distance behind it the dorsal wall of the cord is even thicker than the ventral (Fig. 2.9 C inset). No dorsal crest or dorsal roots are present though the dorsal mesentery is well developed through the collar (Fig. 2.9 C). The collar canals are large and vertically oriented (Fig. 2.9 D, D inset). The collar longitudinal muscles are well developed and form wing-shaped bundles on either side of the collar lumen (Fig. 2.9 D).

The ventral portion of the pharynx is about a third of the size of the branchial portion. The number of branchial pores on each side is probably about 30. Gonads begin somewhat posterior to the middle of the branchial region (Fig. 2.9 F). Individual gonads are well separated from each other and stand out prominently from the surface of the body. Intestinal pores and hepatic caeca are absent.

We carry out Ritter's intention by naming the species for Professor Trevor Kincaid, long of the University of Washington and a pioneer northwestern naturalist.

The defining characters of *Horstia kincaidi* are listed below:

A. Body very tapered, proboscis round
B. Short proboscis and collar
C. Longitudinal musculature of the proboscis in radial plates
D. Deep and narrow skeletal keel with the cornua steeply bent ventral wards at their posterior end
E. The dorsal and ventral mesenteries are present in the proboscis and collar
F. Left or right proboscis pore
G. Anterior neuropore
H. Large vertical collar canals
I. Two rows of lateral gonads forming small protuberances starting in the middle of the branchial region (no genital ridges or wings)
J. Gonopores on an elevated ridge

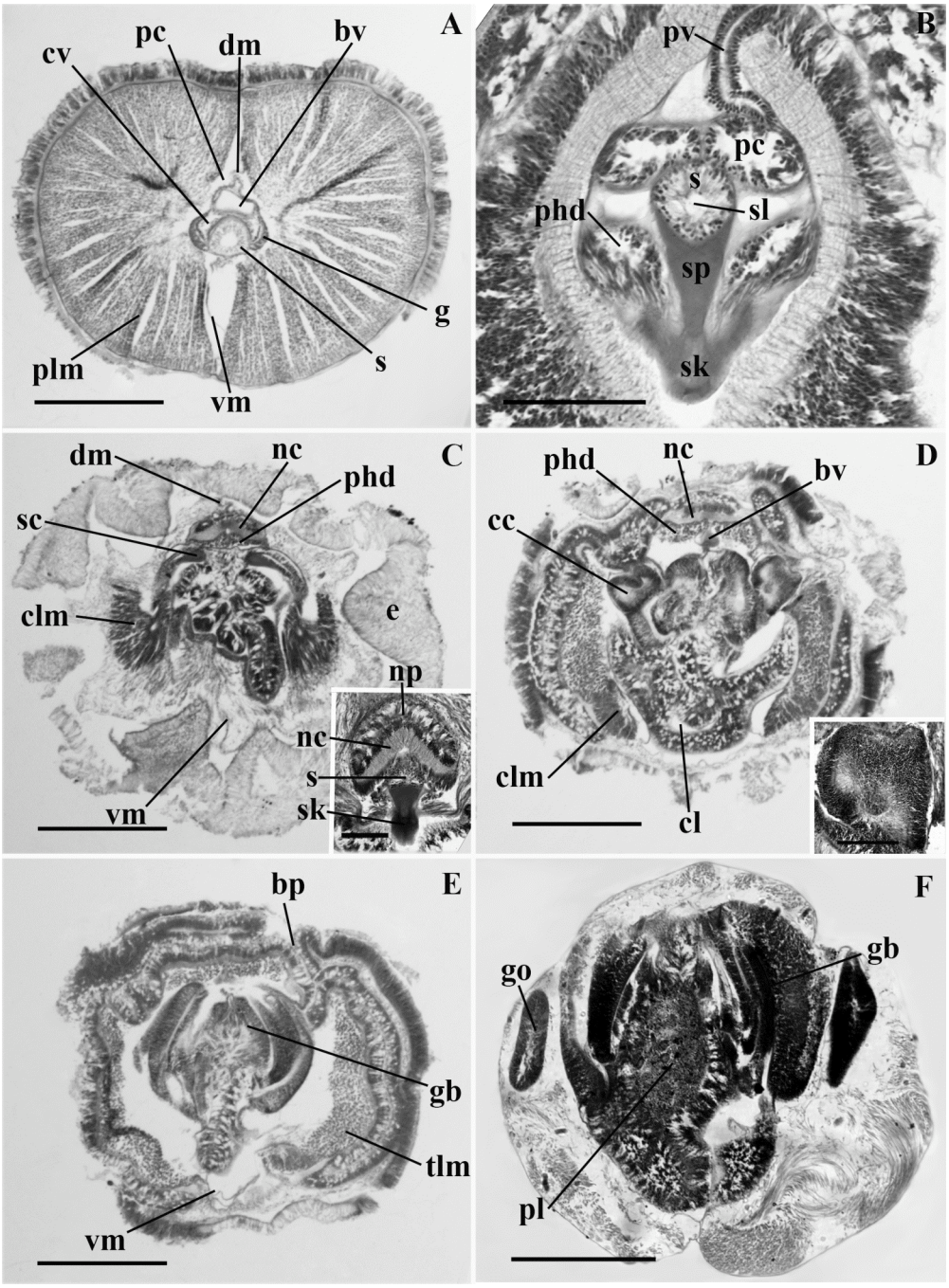

Figure 2.9 Light micrographs of transverse sections of *Horstia kincaidi* n. gen. and sp.. (A) Proboscis with heart-kidney complex. (B) Proboscis neck. (C) Collar, (inset) collar nerve cord and stomochord (D) Anterior pharyngeal region of the trunk, (inset) collar canal. (E) Pharyngeal region of the trunk. (F) Genital region of the trunk. bp, branchial pore; bv, blood vessel; cc, collar canal; cl, collar lumen; clm, collar longitudinal muscles; cv, cardiac vesicle; dm, dorsal mesentery; g, glomerulus; gb, gill bar; go, gonad; nc, nerve cord; np, neuropore; pc, proboscis coelom; phd, perihaemal diverticulum; pl, pharynx lumen; plm, proboscis longitudinal muscles; pv, proboscis vesicle; s, stomochord; sc, skeletal plate; sk, skeletal keel; sl, stomochord lumen; sp, skeletal plate; tlm, trunk longitudinal muscles; vm, ventral mesentery. Scale bars (A, C, E, and G) = 500 µm; (B) = 200 µm; (D and F) = 100 µm; (H) = 300 µm.

DISCUSSION

The present study has provided us the opportunity to evaluate the characters used to distinguish the species, even though such characters are probably of quite unequal reliability. The generic characters (see generic diagnoses and key to the genera) are sometimes used in defining species and are most likely to be stable, independent of environmental influence, season, age and individual variation. It is probably the same for a number of the common trivial characters such as the extent of dorsal and ventral mesenteries, the position of the gonads, the extent of the perihaemal and peribuccal diverticula, the cross sectional shape of the collar canals, the presence of parabuccal ridges, and the development of the skeleton body and cornua. The shape and arrangement of the proboscis complex, including the stomochord, cardiac vesicle, glomerulus and blood vessel is a particularly good character that seems to be stable and reliable. These have been consistent in the few species of which many individuals have been sectioned.

There remain many characters, believed to be diagnostic of species but less validated and difficult to assess. These include the extent of a proboscis groove, the number of muscle rings in the proboscis (*Saccoglossus*), the thickness of the proboscis circular muscle fiber layer with respect to the nerve fiber layer, the opening of neuropore(s), the number and extent of collar nerve cord lacunae and the presence of esophageal pores. It is generally agreed that these have a degree of reliability and hence we have leaned on them in part in the species accounts above. But the point to be stressed here is that this is a tentative and subjective judgment, and that the least confusion in the long run will be caused by erring on the side of recognizing too many taxa. We do not place undue weight therefore on the validity of each species and genus and feel that they should not be lumped without a new and more serious study of the diagnostic characters. Therefore our principal hopes for future validation, correction and improvement in the taxonomy of the harrimaniid enteropneusts are validity tests of present characters and the development of new characters. Because of the low number of

unique features, the addition of one character, shared with some other taxa but not others, could greatly increase the discrimination and definition of each taxon.

ZOOGEOGRAPHY

No general observations can, at this point, be made about the zoogeography of harrimaniid worms. *Protoglossus mackiei, Stereobalanus willeyi, Horstia kincaidi*, *Mesoglossus macginitiei*, and *Ritteria ambigua* are known from single individuals or single lots (Fig. 10) in the collection of specimens studied here. This may be due to a lack of sampling, especially in the subtidal.

Harrimania maculosa is known from Prince William Sound and Kodiak Island, Alaska (Ritter, 1900) and from Providence Bay in eastern Siberia (present study), points 2200 km apart (Fig. 10). Here clearly the lack of effort in searching prevents a meaningful conclusion as to whether the distribution is disjunct and punctate or really a sizeable zoogeographical area of essentially continuous occurrence.

Mesoglossus intermedius is known from points on the central California coast about 200 km apart but not at many seemingly suitable sites in between (Fig. 10) (present study). This may be due to the paucity of visits. Its absence from the rocky, protected outer coast farther north may likewise be due to inadequate search. But its absence from the well-worked coast of southern California is probably real.

Stereobalanus canadensis has a discontinuous distribution that may span two oceans, occuring in the Lower Estuary and Gulf of St. Lawrence, Québec (Brunel *et al*. 1998), including the type-locality east of Prince Edward Island (Spengel 1893, 1901), in New England (Reinhard 1942) and possibly from Southern California (Bullock, personnal communication) (Fig. 10). A possible interpretation of such a stenotopic distribution could be that *Stereobalanus canadensis* populations are relicts of a once wider ranging species.

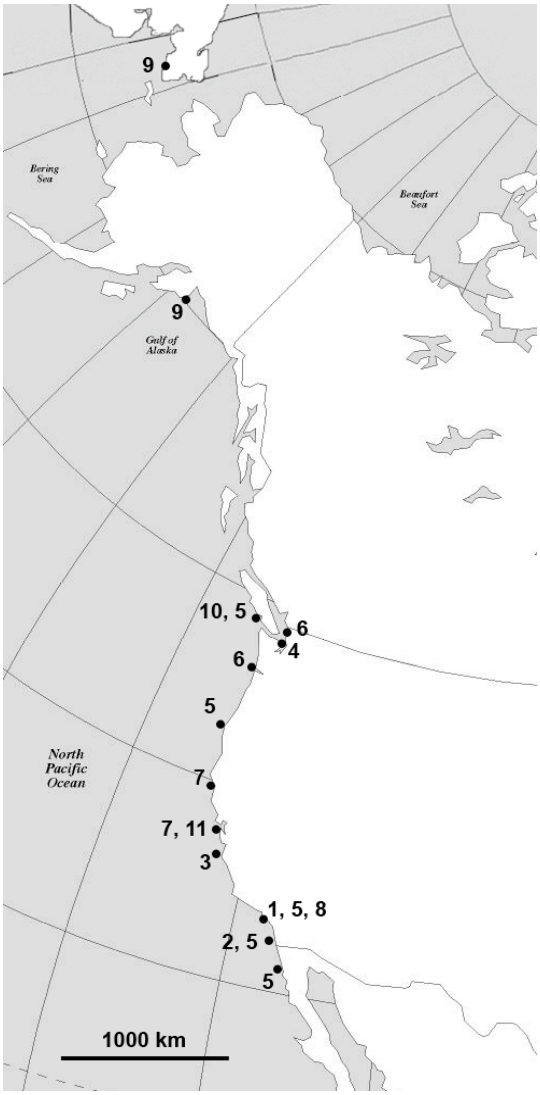

Figure 2.10 A map of the geographic distribution of harrimaniid enteropneusts on the west coast of North America: 1, *Stereobalanus willeyi* **n. sp.** Newport Bay, CA. 2, *Stereobalanus canadensis* San Diego, CA (also found in the Lower Estuary and Gulf of St. Lawrence, including east of Prince Edward Island (type-locality); New England). 3, *Ritteria ambigua* **n. gen. et n. sp.** Monterey, CA. 4, *Horstia kincaidi* **n. gen. et n. sp.** Whidbey Island, WA. 5, *Saccoglossus pusillus* Barkley Sound, BC; Cape Arago, OR; San Pedro, San Diego, La Jolla, Anaheim, Newport Bay, CA; Ensenada, Mexico. 6, *Saccoglossus bromophenolosus* Padilla Bay, Willapa Bay, WA. 7, *Mesoglossus intermedius* **n. gen. et n. sp.** Shelter Cove, Moss Beach, CA. 8, *Mesoglossus macginitiei* **n. sp.** Newport Bay, CA. 9, *Harrimania maculosa* Prince William Sound, Kodiak, AK; Providence Bay, Siberia. 10, *Harrimania planktophilus* Barkley Sound, BC. 11, *Protoglossus mackiei* **n. sp.** Moss Beach, CA.

PHYLOGENY

The phylogenetic hypothesis for the harrimaniid worms was constructed using the 18S rDNA gene tree (Cannon *et al*., 2009) as a backbone, to which we added the new genera *Horstia*, *Ritteria* and *Mesoglossus* using morphological characters (Fig. 2.11). Our tree shows that the proboscis musculature is a good character to define the different groups within the family. Using *Ptychodera* as an outgroup this phylogeny suggests that the radial arrangement of proboscis muscle fibers may be ancestral to the family and that this type of arrangement would have been subsequently lost in *Ritteria*, *Saxipendium*, *Mesoglossus* and *Saccoglossus* (Fig 2.11-J) and replaced by a diffuse or concentrically arranged muscle fibers.

Our data suggests that *Saxipendium* is a close relative of *Ritteria*, another deep-sea genus that has been found at a depth of 700 meters off the coast of California. These species display a diffuse proboscis musculature and have a coronate proboscis skeleton (Fig 2.11-L), a synapomorphy of the group. *Mesoglossus* is more closely related to *Saxipendium* and *Ritteria* than it is to *Saccoglossus*, the genus to which four *Mesoglossus* species were previously assigned. *Horstia* is sister genera to *Protoglossus* and *Harrimania*; all three genera have a radial arrangement of proboscis musculature, a ventral and a dorsal proboscis mesentery.

The hypothesis that *Protoglossus* may be basal among the Enteropneusta based on its simple arrangement of body cavities (Burdon-Jones, 1956) is refuted here because all three species have perihaemal diverticula and *P. koehleri* has rudimentary peripharyngeal diverticula (Table II). Furthermore, the 18S rDNA gene tree (Cannon *et al.,* 2009) and our morphological analysis place *Protoglossus* as sister group to *Harrimania* based on the synapomorphy parabuccal ridges (Fig 2.11-F) that were once thought in *Harrimania maculosa* to be an esophageal notochord (Ritter, 1900). The basal harrimaniid genus *Stereobalanus* has extensive gonadal ridges. They are not as

extensive as the gonadal wings (which possess septa) that characterize the family Ptychoderidae but the reduction of this feature supports the supposition that harrimaniid worm evolution has generally been characterized by a loss of morphological complexity.

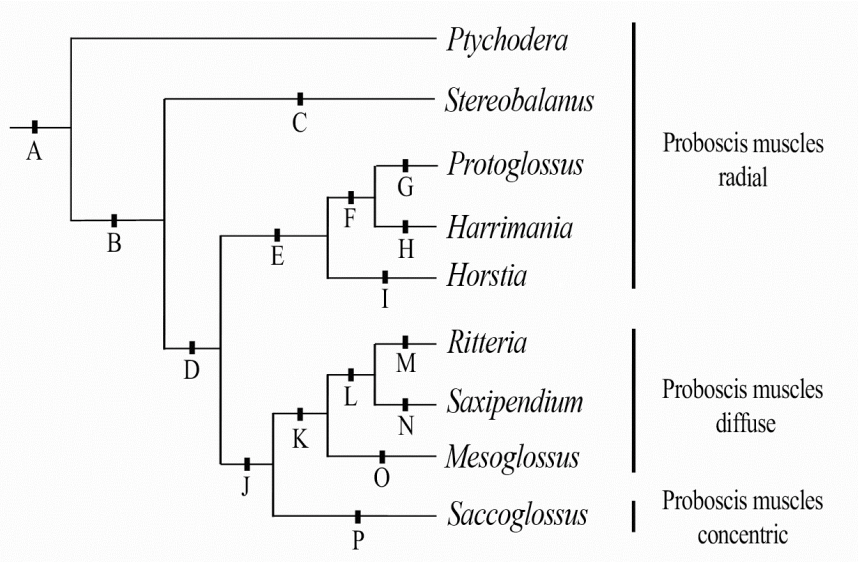

Figure 2.11 A phylogenetic hypothesis for the family Harrimaniidae that was constructed using the tree of Cannon et al (2009) as a backbone, to which were added the new genera *Horstia*, *Ritteria* and *Mesoglossus*. (A) Proboscis longitudinal musculature in radial bundles; (B) Direct development, absence of branchial synapticules, hepatic caeca, genital wings, trunk lateral septa, parabranchial ridges and circular muscles in the trunk; (C) Four tubular genital ridges restricted to the branchial region, reduced proboscis canals and pores; (D) No currently known characters appear to be unique to this group; (E) Dorsal and ventral proboscis septa; (F) Parabuccal ridges; (G) Prominent dorsal proboscis groove, proboscis short and conical, anterior edge of the collar is ruffled, anterior and posterior neuropores, parabuccal ridges extend to the posterior part of the collar, dorsal and ventral septa in the proboscis and collar; (H) Collar broader than long, no peribuccal diverticula, proboscis conical, a little longer than broad; (I) No genital ridges, gill pores on an elevated ridge, proboscis round and as long as broad, trunk very narrow; (J) Loss of radial proboscis longitudinal musculature; (K) Proboscis longitudinal musculature is diffuse; (L) Live in deep sea, coronate proboscis skeleton; (M) Absence of proboscis neck, two pairs of genital ridges, proboscis round, proboscis and collar broader than long, proboscis pore opens into the neuropore; (N) Collar pores, cardiac vesicle attached to the dorsal wall of the proboscis, externally visible gonopores, gill pores not visible externally; (G) Proboscis at least twice as long as broad, diffuse proboscis longitudinal musculature; (P) Proboscis at least twice as long as broad, proboscis longitudinal musculature in concentric rings.

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APPENDIX

Table I. Comparison of external and internal characters of the species of the family Harrimaniidae, excluding members of the genus *Saccoglossus*, which will be discussed in a subsequent paper. Characters from previously described species were either obtained from the literature, or, in the case of *Harrimania maculosa* and *Saxipendium coronatum*, from the literature and the holotypes. Question marks indicate when a character state is unknown.

	Harrimania planktophilus [1]	***Harrimania maculosa*** [2]	***Harrimania kupfferi*** [3]	***Harrimania borealis*** [4]	***Protoglossus graveolens*** [5]	***Protoglossus koehleri*** [6]	***Protoglossus mackiei****	***Horstia kincaidi****	***Ritteria ambigua****
Distinctive characteristics								Body very tapered	No neck
Proboscis shape	Conical	Depressed, Conical	Conical	?	Pointed	Pointed	Conical	Rounded	Short, rounded
Proboscis length: width	Longer than broad	As long as broad	Longer than broad	?	Longer than broad	Longer than broad	Longer than broad	As long as broad	Little longer than broad
Proboscis longitudinal musculature	Radial	Radial	Radial	Radial	Radial	Radial	Radial	Radial	Diffuse
Proboscis coelom	Starts at the tip of proboscis	Anterior filled with connective tissue	Anterior filled with connective tissue	?	Filled with connective tissue	Starts at the tip of proboscis	Starts at the tip of proboscis	Starts at the tip of proboscis	Starts at proboscis complex
Proboscis groove	Dorsal	Dorsal	?	No	Deep dorsal	Deep dorsal	Deep dorsal	Dorsal	Dorsal
Proboscis pores	Left or both	Both	Both	Left	Left	Left	Left	Left or right	Left
Collar length: width	Broader than long	Broader than long	Broader than long	Broader than long	Broader than long	As long as broad	Broader than long	As long as broad	Broader than long
Collar shape	Posterior ruffled	Anterior ruffled	Deep posterior ring	Anterior frilled, posterior raised band	Deep posterior ring, anterior ruffled	Deep posterior ring, anterior ruffled	Anterior ruffled	Posterior ruffled	Posterior expanded rim
Neuropore	Posterior, (anterior)	(Anterior)	Anterior	?	?	Anterior, posterior	Anterior (posterior)	Anterior	Anterior
Nerve crest	?	No	No	No	?	?	No	No	No
Extent of periheamal diverticula	Seperate, in collar only	Seperate, in neck	Seperate, in collar only	Confluent anteriorly 2/3 of collar		To posterior limit of cornua	In neck	In neck	Seperate, in collar only
Peripharyngeal diverticula	No	No	No	No	?	Rudimentary	No	No	No
Skeleton shape	?	?	Funnel shaped plate	?	Plate forms 2 skewed funnels	No well developed keel, concave plate	Well developed keel	Deep and narrow keel	Coronate body
Extent of cornua	Pharynx	Pharynx	Posterior collar	?	Posterior collar	Posterior collar	Posterior collar	Posterior collar	Posterior collar
Presence and extent of parabuccal ridges	Anterior collar	Esophagus	?	Yes	Posterior collar	Posterior collar	Posterior collar	Anterior collar	Anterior collar
Presence and shape of collar canals	?	Short, horizontal	Dorsal fold	Yes	Yes	Yes	Horizontal	Large and vertical	Infolded, horizontal
Proboscis septa	Dorsal, ventral	Not complete	Dorsal, ventral	Ventral	Dorsal, ventral	Dorsal, ventral	Dorsal, ventral	Dorsal, ventral	Ventral
Collar septa	Dorsal, ventral	No	No	Dorsal, ventral	Dorsal, ventral	Dorsal, ventral	Dorsal, ventral	Dorsal, ventral	No
Trunk septa	?	No	Dorsal, ventral	Dorsal, ventral	Dorsal, ventral	Dorsal, ventral	Dorsal	Ventral	Dorsal
Size of branchial pharynx: digestive	Branchial bigger	?	Digestive bigger	?	?	Equal	Equal	Branchial bigger	Equal
Rows of gonads	Lateral	Lateral, dorsal	Lateral, dorsal	Lateral	Lateral	Lateral	Lateral	Lateral	Lateral, dorsal
Genital ridges	Irregular	No	Yes	No	?	Yes	No	No	Yes
Number of gill pores	Up to 54 pairs	40 pairs	40 pairs	30+ pairs	60-143 pairs	14-30 pairs	?	30	?
Gonads start	Posterior pharynx	Behind collar	Anterior gill region	Behind collar	In gill region	Posterior half of collar	?	Posterior half of gill region	Behind collar
Number of esophageal pores	?	?	?	?	0	0	?	0	?
Ventral muscular ridge	Yes	?	?	?	?	?	?	?	Yes

Table I (continued)

	Mesoglossus Macginitiei *	*Mesoglossus intermedius* *	*Mesoglossus bournei* [7]	*Mesoglossus caraibicus* [8]	*Mesoglossus gurneyi* [9]	*Mesoglossus pygmaeus* [10]	*Stereobalanus willeyi* *	*Stereobalanus canadensis* [11]	*Xenopleura vivipara* [12]	*Saxipendium coronatum* [13]
Distinctive characteristics				Gill pores not visible externally			4 columnar gonad ridges in branchial region	4 columnar gonad ridges in branchial region	Medullary folds, internal hepatic caeca	
Proboscis shape	?	Conical	Flattened	Flattened, conical	Flattened	?	Conical	Flattened	Rounded	Arrow shaped
Proboscis length: width	?	Longer than broad	Longer than broad	Longer than broad	Longer than broad	Longer than broad	Longer than broad	Broader than long	?	Longer than broad
Proboscis longitudinal musculature	Diffuse	Diffuse	Not concentric	Not concentric	Diffuse	Diffuse	Radial	Radial	?	Diffuse
Proboscis coelom	Starts at proboscis complex	Starts at proboscis complex	Starts at the tip of proboscis	Starts at the tip of proboscis	?	Starts at the tip of proboscis	Obliterated by tissue	?	Filled with connective tissue	In posterior third of proboscis
Proboscis groove	?	No	Dorsal and ventral on preserved specimens	?	Dorsal and ventral may be present	Fine dorsal	No	?	?	Dorsal
Proboscis pores	Left	Left	Left	Median	Median	Left	Both	Both	Left	Left
Collar length: width	?	Broader than long	Broader than long	As long as broad	Broader than long	Broader than long	Broader than long	Broader than long	?	Broader than long
Collar shape	?	Anterior ruffled, posterior ring	3 rings	?	?	?	Anterior expanded rim	Flattened	?	Posterior ring
Neuropore	Anterior, posterior	(Anterior)	Anterior	No	Anterior	?	Posterior	?	Anterior, posterior	Anterior, posterior
Nerve crest	Yes	No	?	No	No	No	No	?	?	No
Extent of perihaemal diverticula	Confluent anteriorly, in neck	In collar only	?	Do not reach anterior collar	?	Posterior collar	In neck	In neck	?	In neck
Peripharyngeal diverticula	Yes	No	No	Yes	?	Yes	No	No	?	No
Skeleton shape	Mid-dorsal ridge	Well developed keel	?	Body bears a spine	?	?	No keel	Plate flat, broad blunt keel	?	Plate coronate, no keel, cornua recurved
Extent of cornua	2/3 collar	Posterior collar	Posterior collar	Mid-collar	Not to anterior collar	Posterior collar	Posterior collar	Posterior collar	?	Posterior collar
Presence and extent of parabuccal ridges	No	No	Posterior collar	?	Posterior collar	?	No	?	Trunk	No
Presence and shape of collar canals	Short, vertical	Short, vertical	?	Dorsal fold	?	Oval, no fold	No	No	Elongate	with collar pores
Proboscis septa	Ventral	Ventral	Ventral	Ventral	?	Ventral	Ventral	Ventral	Dorsal, ventral	Pericardiac vesicle in contact with dorsal wall, ventral
Collar septa	Dorsal, ventral	Dorsal, ventral	Dorsal, ventral	Dorsal, ventral	Dorsal, ventral	Dorsal, ventral	?	Ventral	?	Dorsal
Trunk septa	no	?	?	?	?	?	?	Dorsal, ventral	?	Dorsal, ventral
Size of branchial pharynx: digestive	Branchial bigger	Equal	Branchial bigger	Branchial bigger	?	?	Branchial bigger	Equal	?	Branchial bigger
Rows of gonads	Lateral	Lateral	?	?	?	?	Lateral, dorsal	Lateral, dorsal	?	Lateral
Genital ridges	Yes	No	No	?	No	?	Yes	Yes	No	Yes
Number of gill pores	?	25 pairs	?	50 pairs	?	9-22 pairs	70 pairs	?	4 pairs	54 pairs
Gonads start	Behind collar	2mm behind collar	Behind collar	?	?	Behind gill region	In gill region	In gill region	Behind collar	Behind collar
Number of esophageal pores	?	?	?	?	0	1 pair	1 pair	?	1 pair	40 pairs
Ventral muscular ridge	Yes	No	No	?	?	No	Yes	?	?	No

* New species; 1. Cameron, 2002; 2. Ritter, 1900; 3. van der Horst, 1939; 4. Okuda & Yamada, 1955; 5. Giray & King, 1996; 6. Caullery & Mesnil, 1900, 1904; 7. Menon, 1904; 8. van der Horst, 1924; 9. Robinson, 1927 and van der Horst, 1939; 10. Hinrichs and Jacobi, 1938; 11. Spengel, 1893; l2. Gilchrist, 1925; 13. Woodwick & Sesenbaugh, 1985

Table II. A dichotomous key to the enteropneust families Harrimaniidae, Spengelidae, Ptychoderidae and Torquaratoridae and to the genera of family Harrimaniidae.

1	Proboscis short, ovate; collar shorter than broad, hepatic caeca present in some genera; proboscis muscle includes thick layer of circular muscle encompassing homogenously arranged longitudinal fibers; stomochord with a vermiform process; pericardium and glomerulus with paired anterior diverticula more or less developed; chondroid tissue well developed; eggs small.....	family Spengeliidae
	- Stomochord with no vermiform process; pericardium simple; ventral part of pharynx large and sometimes more or less separated from the branchial part.....	2
2	- Proboscis short, hepatic caeca, genital wings.....	3
	Proboscis short or elongate, round or conical; collar peribuccal cavities absent, nerve-roots rarely present; skeletal cornua extending at least to middle of collar; trunk lacks circular muscles, lateral septa, parabranchial ridges, synapticles, and hepatic caeca; development direct, eggs large.....	4, family Harrimaniidae
3	Proboscis short, conical; collar as long as broad with nerve roots; trunk external regionation pronounced; ventral part of pharynx large and sometimes more or less separated from branchial part by parabranchial ridges; genital wings extend into esophageal region; hepatic caeca ear-shaped; proboscis muscle in radial pattern of bands; gill bars short, curved, with synapticules; parabranchial ridges present; longitudinal ciliated intestinal grooves; eggs small, development indirect via tornaria larva.....	family Ptychoderidae
	- Proboscis short, dome shaped; collar very broad with midventral slit; short skeletal cornua; hepatic caeca; genital wings, gill bars without synapticules; eggs large.....	Family Torquaratoridae
4	Proboscis longitudinal musculature in radial plates.....	5
	- Proboscis longitudinal musculature not in radial plate.....	8
5	Four tubular genital ridges restricted to branchial region, proboscis canals and pores reduced or absent.....	*Stereobalanus*
	- Gonads extending at least to oesophageal region, proboscis canals and pores well developed	6
6	Proboscis conical, parabuccal ridges.....	7
	- Proboscis round, trunk very narrow, gill pores on an elevated ridge.....	*Horstia*
7	Proboscis with deep posterior dorsal groove, anterior edge of the collar is ruffled, anterior and posterior neuropores, parabuccal ridges extend to the posterior part of the collar, dorsal and ventral septa in the proboscis and collar.....	*Protoglossus*

	- Proboscis a little longer than broad, no peribuccal diverticula, sometiimes four rows of gonads and two proboscis pores, cornua may extend into the trunk.....	*Harrimania*
8	Proboscis at least twice its width with middorsal longitudinal groove and muscles arranged in several concentric rings.....	*Saccoglossus*
	- Proboscis longitudinal musculature arranged diffusely.....	9
9	Dorsal trunk with medullary folds; viviparous.....	*Xenopleura*
	- No medullary folds; oviparous.....	10
10	Proboscis skeleton plate coronate.....	11
	- Prooscis plate not coronate, proboscis twice its width, no conspicuous dorsal groove.....	*Mesoglossus*
11	Proboscis neck, proboscis skeleton without a keel, two genital ridges, collar canals with pores leading directly to the exterior of the body, cardiac vesicle attached to dorsal the wall of the proboscis, externally visible gonopores, gill pores not visible externally.....	*Saxipendium*
	- No proboscis neck, proboscis skeleton with keel, collar broader than long, proboscis pore opens into the neuropore, four genital ridges.....	*Ritteria*

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5. Discussion

5.1 VALIDITÉ DES CARACTÈRES TAXONOMIQUES

Nous sommes conscients du risque d'établir de nouvelles espèces qui n'en sont pas réellement, mais nous croyons qu'il vaut mieux risquer une certaine confusion en accordant de l'importance à certains caractères peut-être sans importance en réalité, plutôt que d'ignorer ces différences. Nous croyons qu'il sera plus simple, s'il y a lieu ultérieurement, de mettre deux espèces en synonymie que d'en créer de nouvelles, vu l'ampleur du travail requis pour la préparation des spécimens et leur description.

Nous avons aussi conscience que de nombreux facteurs pourraient ajouter de l'incertitude aux descriptions anatomiques présentées ici. En fait, la distribution des caractères morphologiques permettant l'identification des différents groupes taxonomiques est ambiguë, principalement parce que les espèces, les genres et les familles diffèrent généralement les uns des autres par une combinaison unique de caractères et par la présence ou l'absence de structures observées sur des coupes histologiques. Peu de structures sont en elles-mêmes distinctives. Comme les entéropneustes possèdent peu de structures rigides, la distorsion lors des coupes et de la fixation peut créer des artéfacts. En raison de la rareté des spécimens, les descriptions ont souvent été faites à partir de spécimens uniques. De plus, jusqu'à maintenant très peu d'informations sont disponibles au sujet des variations ontogénétiques, phénotypiques ou environnementales. Nous croyons quand même que ce projet permettra d'identifier plusieurs caractères diagnostiques et apportera beaucoup de connaissances sur la classe des entéropneustes.

L’examen des coupes histologiques, surtout celles des espèces représentées par plusieurs spécimens, nous a permis de compiler plus d’une trentaine de caractères morphologiques internes et externes qui semblent stables. Ces résultats furent ensuite comparés aux descriptions d'espèces provenant de la documentation et nous ont permis de déterminer quels étaient les meilleurs caractères anatomiques disponibles pour l'identification des espèces (voir Table 1).

Nous espérons que la clarification des divers états de caractères sera utile aux chercheurs qui tentent de répondre aux questions sur l'évolution des entéropneustes et des deutérostomiens.

5.2 PHYLOGÉNÉTIQUE

En raison du manque de caractères exclusifs à chaque taxon, à cette étape-ci du projet, une analyse phylogénétique avec comme unique base la matrice de caractères présentée plus haut (Table I) mène à une phylogénie sans résolution. C'est pour cette raison que nous nous sommes basés sur l'arbre obtenu à partir de l'ARN 18S (Cannon *et al*., 2009) pour élaborer notre hypothèse phylogénétique.

Nous avons ajouté à l'arbre moléculaire les trois nouveaux genres *Horstia*, *Ritteria* et *Mesoglossus* en utilisant les caractères morphologiques illustrés dans la figure 2.11 et décrits dans le tableau I. L'arbre obtenu montre que l'arrangement des muscles du proboscis semble être un caractère utile à la définition des divers groupes au sein de la famille. C'est d'ailleurs par ce caractère que plusieurs genres se différencient les uns des autres. Notre hypothèse suggère aussi que la musculature radiale pourrait être l'état de caractère ancestral des Harrimaniidae et que ce type d'arrangement aurait pu être perdu par la suite chez *Ritteria*, *Saxipendium*, *Mesoglossus* et *Saccoglossus*. Il serait maintenant intéressant de voir où se place la famille des Spengelidae dans la phylogénie, afin de comprendre l'évolution de la musculature du proboscis, puisque la musculature est diffuse dans cette famille.

Selon nos résultats, le genre *Saxipendium* trouvé près des sources hydrothermales des îles Galapagos et transféré ici dans la famille des Harrimaniidae, serait un proche parent de *Ritteria*, un genre monospécifique provenant aussi de grandes profondeurs marines. Chez les deux espèces, la muculature du proboscis est diffuse et le squelette du proboscis est de forme coronaire. Ce dernier caractère est jusqu'à présent exclusif à ces deux espèces, mais il serait intéressant de voir si le squelette d'autres espèces des

profondeurs marines ont cette forme particulière et si ce caractère pourrait être une adaptation au mode de vie en mer profonde.

Il est aussi intéressant de remarquer que le genre *Mesoglossus* serait plus proche parent de *Saxipendium* et *Ritteria* que de *Saccoglossus*, genre duquel quatre espèces de *Mesoglossus* ont été soustraites.

Finalement, notre analyse réfute l'hypothèse de Burdon-Jones (1956) selon laquelle *Protoglossus* serait un groupe basal au sein des Harrimaniidae en raison de l'arrangement simple de ses cavités coelomiques. En effet, le présent travail montre que les espèces de ce genre possèdent des cavités périhémales, qu'une espèce possède des diverticules pharyngiens et que les mésentères du tronc ne sont pas complets chez tous les membres du groupe. *Protoglossus* serait en fait le groupe frère de *Harrimania* avec lequel il partage la présence de crêtes parabuccales.

5.3 ZOOGÉOGRAPHIE

Il nous est pour le moment impossible d'apporter de nouvelles conclusions au sujet de la répartition géographique des Harrimaniidae. Nos données semblent suggérer que certaines espèces ont une distribution discontinue et plusieurs hypothèses peuvent expliquer ce fait. Par exemple, l'absence ou la rareté des échantillons dans certaines régions, particulièrement dans l'étage infralittoral et l'absence d'habitat convenable ou la modification de ces habitats le long des côtes pourraient expliquer cette distribution sténotopique. Toutefois, selon une autre interprétation, certaines espèces comme *Stereobalanus canadensis* qui semblent présentes de part et d'autre du continent américain, pourraient avoir eu une distribution ancienne continue et plus grande qui aurait été fragmentée par la suite.

5.4 SUITE DU PROJET

D'autres descriptions sont déjà en cours pour compléter l'ensemble des nouvelles espèces de la famille Harrimaniidae provenant de la collection de Ritter et Bullock. Il s'agit de 5 espèces du genre *Saccoglossus* dont les descriptions seront publiées ultérieurement. Avec ces descriptions, le nombre d'espèces nord-américaines sera porté à 39. Toutefois, il serait imprudent d'affirmer que la diversité réelle des entéropneustes est en voie d'être connue. Cette affirmation se base d'abord sur le fait que la collection sur laquelle nous travaillons actuellement recèle encore de nombreux spécimens non identifiés. De plus, les côtes de l'Amérique du nord n'ont pas toutes été fouillées, plus particulièrement les eaux plus profondes et plus nordiques. D'ailleurs, aucun spécimen provenant de l'Alaska n'a été rapporté depuis *Harrimania maculosa* au dédut du siècle dernier (Ritter & Davis, 1904). Il n'est donc pas difficile de croire que ces eaux recèlent davantage d'espèces.

Au cours des observations effectuées sur les spécimens de la famille Ptychoderidae, qui feront partie d'une publication ultérieure, une nouvelle structure qui semble présente chez tous les spécimens de la famille a été identifiée. Il s'agit d'un complexe vascularisé qui se trouve dans la partie ventrale du collet. Il serait intéressant d'observer l'ultrastructure de ce complexe au microscope électronique à transmission, afin de tenter d'en comprendre la fonction.

5.5 PERSPECTIVES

Dans le contexte environnemental actuel, avec la destruction des habitats et la surexploitation des ressources, les extinctions d'espèces augmentent et les écosystèmes de la planète se retrouvent en plein changement. La taxonomie devient alors un outil essentiel pour répondre aux préoccupations liées à la gestion de la biodiversité. Pour conserver la biodiversité, il faut bien connaître les espèces et pouvoir les identifier correctement. La taxonomie est d'autant plus importante pour permettre l'enrichissement de l'inventaire de la biodiversité mondiale.

Ces descriptions d'espèces pourront éventuellement contribuer à cet inventaire de biodiversité et aider, entre autres, les gouvernements à implanter des aires marines protégées, puis permettre l'identification d'espèces indicatrices ou envahissantes.